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Neural correlates of vocal learning in songbirds and humans

Kant, A.M. van der

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Author: Kant, Anne Marie van der

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CHAPTER 1

General introduction

Animal models, songbirds particularly, are increasingly used to study the human capacity for speech and language. In the light of understanding both language evolution and individual language acquisition these models are highly valuable, provided that they are studied within a valid comparative framework. In the past few decades, non-invasive methods such as functional Magnetic Resonance Imaging (fMRI) and Near-InfraRed Spectroscopy (NIRS) have become available for human as well as animal brain research. In the studies discussed in this thesis, fMRI is employed to unravel the neural correlates of vocal learning in the human and songbird brain. The rationale for this route towards a better understanding of the human language capacity will be outlined in this introduction, exploring both (1) how cross-species comparative research, especially comparisons between humans and songbirds, can inform questions about human language acquisition and (2) how recently developed non-invasive neuro-imaging techniques can contribute to our understanding of the neural substrates of vocal learning in general and the human capacity for language in particular.

This introduction is based on the paper "Inter-species comparative research in vocal learning: possibilities and limitations" by Anne van der Kant, published in the Student Volume of the 9th International Conference on the Evolution of Language, 2014

1.1 What can birdsong learning teach us about human language?

1.1.1 The value of the songbird model for human speech

Human language is widely regarded as the pinnacle of the uniqueness of human cognition within the animal kingdom. This is a valid standpoint in so far that only humans show evidence of the ability to develop and use a communication system showing the full complexity of human language. However, other animal species do possess the ability for vocal communication and vocal learning, although we have to search outside the primate lineage to find species with these abilities (Egnor & Hauser, 2004). Songbirds share the ability to learn their communicative signals through vocal imitation with humans and a small number of other species (e.g. hummingbirds (Baptista & Schuchmann, 1990), parrots (Pepperberg, 2002), cetaceans (Reiss & McCowan, 1993), pinnipeds (Ralls, Fiorelli, & Gish, 1985; Sanvito, Galimberti, & Miller, 2007), bats (Janik & Slater, 1997) and possibly elephants (Poole, Tyack, Stoeger-Horwath, & Watwood, 2005)). With approximately four thousand species, oscine songbirds represent the largest group of vocal learners in the animal kingdom. These songbirds learn to produce their song by imitating the vocalizations of their male adult conspecifics.

Most species that show vocal learning differ greatly from humans in evolutionary descent, brain and behavior. The limited vocal learning abilities in primates, our closest relatives, complicate the study of vocal learning from the perspective of common descent. Moreover, birdsong, which is the most studied model for human language, is highly limited in its productivity and does not show symbolic representation or duality of patterning like human language (Hockett, 1963). Furthermore, human language is characterized by its capacity to express and combine meaning in an unrestricted way. In contrast, birdsong can have different functions, including mate attraction and territorial defense, which are not coupled to the acoustic content of the song. Although songbirds have been claimed to show some combinatorial potential (e.g. Gentner, Fenn, Margoliash, & Nusbaum, 2006), these findings are controversial (Stobbe, Westphal-Fitch, Aust, & Fitch, 2012; Van Heijningen, De Visser, Zuidema, & Ten Cate, 2009). These factors limit the possibilities for the extrapolation of findings from birdsong studies to the study of human language.

However, birdsong learning, especially in the zebra finch (*Taeniopygia guttata*), does show some striking parallels with the way in which human infants acquire their native language. More specifically, several aspects of the zebra finch song learning process, among others the memorization of the target song during the sensory phase (Eales, 1985) and motor practice or 'babbling' during the sensorimotor phase (Marler, 1970), are comparable to processes which were observed in human speech learning (Doupe & Kuhl, 1999). Furthermore, zebra finches as well as humans are hypothesized to be age-limited learners,

implying that they both need to be exposed to adult vocalization within a specific sensitive period during development in order to develop normal song or language. By focusing on these characteristics of development, songbird studies can add to the understanding of neural mechanisms underlying the development of speech in human infants and of vocal learning in humans as a species. Many other aspects of language, like the capacity for symbolic reference, can be found in other lineages like parrots (e.g. Pepperberg, 2002) and non-human primates (Pollick & De Waal, 2007).

Although non-human primates do not show vocal imitation learning, they do exhibit comprehension learning and usage learning (e.g. alarm calls in vervet monkeys (Seyfarth, Cheney, & Marler, 1980)). The study of apes and monkeys can add to the understanding of human language development in several ways. They can serve as a non-vocal imitation learning control species when comparing vocal learning in humans and birds and additionally they can provide insights into other behaviors that might have contributed to human language evolution, such as auditory processing (Petkov, Kayser, Augath, & Logothetis, 2006), gesture (Pollick & De Waal, 2007), joint attention (Carpenter & Tomasello, 1995) and symbolic reference (Ribeiro, Loula, De Araújo, Gudwin, & Queiroz, 2007). Because chimpanzees and bonobos are our closest relatives, some of the general learning mechanisms they possess may share their evolutionary origin with learning mechanisms that were adapted to sub-serve language in human evolution. By comparing humans to both songbirds and non-human primates, mechanisms we might have in common with either vocal learners or non-vocal learners can be identified.

Studies of animal analogues of capacities needed for human language can complement each other in order to establish which shared cognitive mechanisms underlie the human capacity for language. Because animal studies allow for manipulation of different environmental and developmental factors, both behavioral and neural mechanism can be studied in isolation, which is very difficult to accomplish in human studies. By studying behavioral mechanisms that have been shown to be comparable between species as opposed to attempting to compare complete communication systems, birdsong research has the potential to uncover mechanisms underlying human language that are highly challenging to study in humans.

However, because cognitive mechanisms underlying vocal behavior and auditory processing in songbirds and humans originate from highly dissimilar avian and mammalian brains, comparative studies should take brain function into consideration. Possible approaches that take this issue into consideration are discussed in the second section of this introduction. The studies discussed in the present thesis aspire to develop an understanding of the similarities and differences between the neural processing of learned species-specific vocalizations in avian and mammalian vocal learners.

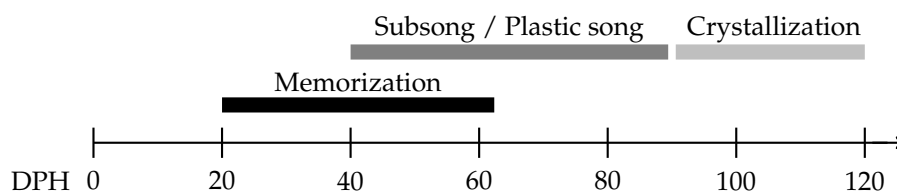


Figure 1.1: Stages of song learning in zebra finches. Memorization of the tutor song starts before juveniles start producing subsong. During the sensorimotor phase juveniles produce subsong and plastic song and use auditory feedback in order to match their vocalizations to the memory of the tutor's song. At the end of the song learning process, one song is crystallized and will be sung by the bird for the rest of its life. DPH = Days Post Hatching.

1.1.2 Learning by imitation in songbirds and humans

Songbirds as well as human infants acquire their species-specific communicative signals by vocal imitation learning. This process involves (i) a preference for species-specific and in particular the parents' vocalizations from a very early developmental stage, (ii) memorization of the vocalizations of adult conspecifics, (iii) motor practice where the juvenile bird or human infant practices sounds that were memorized and (iv) the use of auditory feedback in order to compare one's own vocalizations with the memorized adult vocalizations. Evidence for each of these elements has been found in songbirds as well as in humans.

In order to learn the speech or song of their adult conspecifics, both human infants and juvenile songbirds need to know which sounds to imitate. Evidence for such an innate preference for species-specific vocalizations has indeed been found. Human babies prefer the language spoken by their mother from very early on (Moon, Cooper, & Fifer, 1993). Although macaques do not imitate vocalizations, some auditory regions in the macaque temporal lobe are selectively activated by conspecific sounds and even by the voice of individual conspecifics (Petkov et al., 2008). These results suggest that some brain functions that are important in vocal learning were in place before vocal imitation developed in the human lineage. Zebra finches show a preference for conspecific vocalizations even when reared in isolation (Braaten & Reynolds, 1999). Furthermore, auditory fMRI studies in zebra finches, have shown selectivity for conspecific song and the song of individual birds in the auditory midbrain nucleus, the avian homologue of the inferior colliculus (Poirier, Boumans, Verhoye, Balthazard, & Van der Linden, 2009; Van der Kant, Derégnaucourt, Gahr, Van der Linden, & Poirier, 2013) (see also Chapter 3).

Studies in human infants as well as in juvenile zebra finches suggest that they not only prefer, but also memorize adult vocalizations. Newborns can discriminate familiar stories that were read to them in the womb from unfamiliar stories (DeCasper & Spence, 1986), while the zebra finch brain shows selectivity for the tutor song (usually the father's), even in adulthood (see

Chapter 3 or Van der Kant et al. (2013)). Further evidence for a memory of the tutor's song comes from the fact that male zebra finches are able to produce a highly accurate copy of the adult song they were exposed to during the sensory phase of song learning (Figure 1.1), even if the song model is no longer present during vocal motor practice (Funabiki & Konishi, 2003). However, for the memorization of adult vocalizations, purely the presence of conspecific speech or song is not sufficient. Social interaction is highly important for vocal learning in both humans and songbirds. Human infants benefit from joint attention during social interactions with adults for the development of their vocabulary (Tomasello & Farrar, 1986). The same holds true for zebra finches, for which live tutoring or tutoring with a plastic model bird (Beecher & Burt, 2004) leads to better imitation compared to tape tutoring (Ten Cate, 1991) or operant tutoring (for a comparison of different methods, see Derégnaucourt, Poirier, Van der Kant, Van der Linden, & Gahr, 2013). This suggests that attention plays a large role in the ability to memorize adult vocalizations.

Both the production of birdsong and human speech start with a phase where repetitive strings of unstructured vocalizations are produced that increasingly resemble adult speech sounds or song notes. In songbirds this is known as subsong (Marler, 1970), which is produced early in the sensorimotor phase of song learning (Figure 1.1), while it is referred to as babbling in human infants. Babbles or subsongs are produced independently of a specific social context (Lenneberg, Rebersky, & Nichols, 1965) and develop around the same developmental stage in both normal hearing and hearing-impaired infants (Stoel-Gammon & Otomo, 1986). Babbling thus appears to be a form of vocal motor practice that develops spontaneously and is only later influenced by social interaction (Goldstein, King, & West, 2003) and auditory feedback. Babbling behavior appears to be common among vocal learning species as it was also shown in bats (Knörnschild, Behr, & Von Helversen, 2006).

During babbling and subsequent phases of song and speech learning, auditory feedback plays an important role in the development of adult vocalizations. Auditory feedback is needed in order to evaluate whether one's own vocalizations match the memory of the tutor song (in birds) or adult speech sounds (in babies). Both in songbirds and human infants, the absence of auditory feedback impairs vocal learning. Congenitally deaf babies initially start to vocalize, but fail to develop more structured vocalizations with true consonants due to the absence of auditory feedback (Stoel-Gammon & Otomo, 1986). Furthermore, song development is heavily compromised if songbirds are denied auditory feedback after sensory learning (Konishi, 1965), despite the presence of a fully formed memory of the tutor song. Studies on acquired deafness in humans (Cowie, Douglas-Cowie, & Kerr, 1982) and deafening (Nordeen & Nordeen, 1992) as well as perturbation of auditory feedback (Leonardo & Konishi, 1999) in songbirds have demonstrated that auditory feedback is not only crucial for song and speech learning, but also for its subsequent maintenance.

1.1.3 Sensitive periods for birdsong learning and human language acquisition

As discussed in the previous sections, songbird studies addressing vocal learning behavior have revealed a number of striking similarities with human language acquisition, which have contributed to our understanding of learned vocalizations. An important parallel on which this thesis focusses is the existence of a sensitive period for vocal learning in both humans (Lenneberg, Chomsky, & Marx, 1967) and some songbirds (Eales, 1985). This "sensitive period hypothesis" is supported by a number of findings from both birdsong and human speech.

For human speech, support for the sensitive period hypothesis is predominantly based on individual cases. Theoretically, the hypothesis can be tested by withholding a child spoken language from birth and ask whether this child develops spoken language on its own. Because of the cruelty in such an isolation experiment, it cannot be carried out in humans and isolation studies are limited to case studies of children who grow up isolated from human contact. Recent studies addressing the language capacities of such a "wild" child have shown that absence of human language input impedes the development of spoken language and especially normal syntax (e.g. Curtiss, Fromkin, Krashen, Rigler, & Rigler, 1974; Fromkin, Krashen, Curtiss, Rigler, & Rigler, 1974). Moreover, the spoken language abilities of prelingually deaf children who receive a cochlear are related to the age at implantation (Nikolopoulos, O'Donoghue, & Archbold, 1999). Another indication for a sensitive period for language acquisition with a high level of plasticity early in life comes from the finding that infants perceive small differences between both native and non-native speech sounds, while perception becomes increasingly categorical with a tendency to place non-native speech sound in native categories during the first year of life (Werker & Tees, 1983). Furthermore, second language acquisition is known to proceed with less effort and more successfully at younger ages (e.g. Johnson & Newport, 1989), though the loss of vocal learning ability appears to be more gradual than previously assumed (Hakuta, Bialystok, & Wiley, 2003).

Songbird species differ considerably in the timing of their song learning. Seasonal learners, like starlings (Eens, Pinxten, & Verheyen, 1992), exhibit a period of plasticity at the start of each breeding season, where they start to sing more often and add new songs to their repertoire, while open-ended learners, like canaries (Nottebohm & Nottebohm, 1978), are able to continuously learn new songs throughout their lives. Zebra finches, however, show a pattern that is more similar to human spoken language development, where they learn their song early in life and must be exposed to adult vocalizations within a restricted time window of approximately 120 days, the sensitive period for song learning, in order to develop normal song (Eales, 1985). When reared in isolation of adult song, zebra finches develop an abnormal "isolate" song (Thorpe, 1958). There are some instances in which the song can change,

including deterioration due to deafness (Nordeen & Nordeen, 1992) or adaptation to distorted auditory feedback (Leonardo & Konishi, 1999). Furthermore, a prolongation of the sensitive period was observed in birds that showed incomplete learning at the end of the period after which zebra finch song is usually fully developed (Derégnaucourt et al., 2013).

The behavioral phenotypes of the sensitive periods for vocal learning in songbirds and humans show some interesting similarities. Furthermore, sensitive periods are not unique to vocal learning, but are widespread during the development of sensory systems, among which binocular vision (e.g. Mower, 1991) is the best known example. This raises the question whether the nature and timing of these sensitive periods is governed by domain-general neural mechanisms, which may be shared between species.

1.1.4 Different brains, similar mechanisms?

Both vocal imitation learning and the presence of a sensitive period for vocal learning are shared between songbirds and humans. These similarities suggest that both species have an innate predisposition for vocal learning, possibly originating from shared neural mechanisms. However, large differences in brain anatomy pose challenges to comparative brain research in songbirds and humans. When conducting comparative research, addressing the neural mechanisms underlying vocal learning in songbirds and humans, the large structural differences between the mammalian and avian brain have to be taken into consideration. The bird brain does not have a cortex and is structured in nuclei rather than lamina. Moreover, different views exist as to how the bird brain and the mammalian brain evolved from a common ancestor, implicating different homologies between brain structures (Jarvis et al., 2005). The different structures of the zebra finch brain that are implicated in song learning and production are further illustrated in Figure 1.2 and the regions supporting language functions in the human brain are depicted in Figure 1.3.

However, despite the lack of consensus about the common descent of specific neural structures, functional analogies can inform theories about convergence on the neural level which might underlie the parallels in vocal learning behavior. For example, the brain of vocal learning songbirds as well as the human brain show neural pathways for the processing and production of learned vocalizations, which are not found in avian and primate species without vocal learning capacities (e.g. Jarvis, 2004; Petkov & Jarvis, 2012). Furthermore, recent studies have shown similarities in gene expression between songbird and human brains in regions related to vocal learning (e.g. Pfenning et al., 2014). For example, Hara, Rivas, Ward, Okanoya, and Jarvis (2012) compared levels of parvalbumin (PV), a calcium binding protein in vocal learning and non-vocal learning birds and found significant differences in PV expression between distantly related avian vocal learners and non-vocal learning species. These findings suggest that the neural architecture for vocalization in species which show vocal learning is fundamentally different from the neural

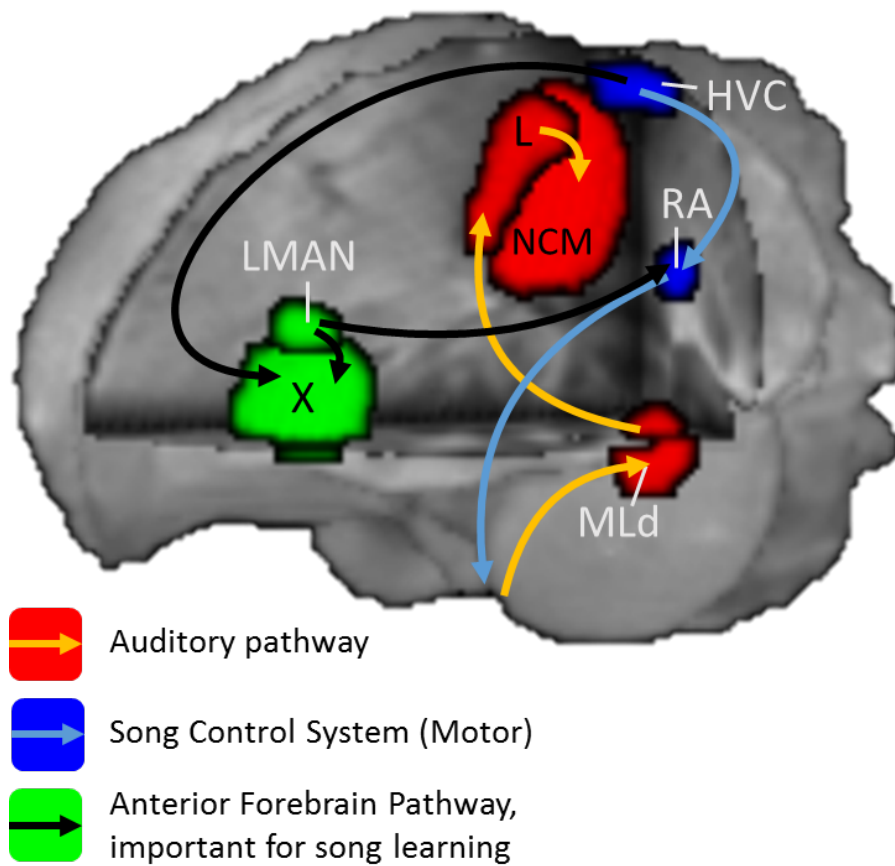


Figure 1.2: Songbird brain regions implicated in singing, song processing and song learning. MLd: Lateral Mesencephalic Nucleus, avian homologue of ICC, L: Field L, primary auditory area, NCM: Caudomedial Nidopallium, secondary auditory area, HVC: Song production planning, RA: nucleus Robustus of the Arcopallium, song motor nucleus, X: Area X, LMAN: Lateral Magnocellular nucleus of the Anterior Nidopallium. Area X and LMAN are part of the Anterior Forebrain Pathway, the pathway linked to song learning.

architecture of non-vocal learning species, even if they are phylogenetically close.

Moreover, the songbird brain exhibits a specialized forebrain circuit, which plays a crucial role in birdsong learning (Brainard & Doupe, 2000; Sohrabji, Nordeen, & Nordeen, 1990) and possibly subserves the generation of subsong (Aronov, Andalman, & Fee, 2008), but is not necessary for adult song production (Nordeen & Nordeen, 1993). This circuit shows similarities with the human basal ganglia, which have recently been found to be functionally connected to regions important for language processing (Booth, Wood, Lu, Houk, & Bitan, 2007) and to be implicated in syntactic processing (Kotz, Frisch, Von Cramon, & Friederici, 2003).

Adult production of birdsong and possibly speech are subserved by neural networks distinct from those that subserve vocal learning (see Figures 1.2 and 1.3). In contrast to juvenile babbling or subsong, adult song production allows for monitoring of vocalizations, but is limited in its experience-dependent plasticity (Brainard, 2004). This mechanism is supported by the finding that adult monkeys, birds and humans all show suppression of auditory neurons during own vocalizations (Eliades & Wang, 2008; Houde, Nagarajan, Sekihara, & Merzenich, 2002; Müller-Preuss & Ploog, 1981; Numminen, Salmelin, & Hari, 1999). The involvement of brain regions that allow for a reduced experience dependent plasticity of vocalizations might underlie sensitive periods for vocal learning in both songbirds and humans.

Furthermore, the genome of the zebra finch has recently been sequenced (Warren et al., 2010), showing striking similarities between these birds and humans with regard to genes involved in vocal communication. This work sets the stage for further studies into the genetic basis of vocal learning, showing the involvement of FoxP2, in zebra finch song learning (e.g. Haesler et al., 2007; Teramitsu, Poopatanapong, Torrisi, & White, 2010). Defects in FoxP2 have previously been associated with an inherited speech disorder in humans (Lai, Fisher, Hurst, Vargha-Khadem, & Monaco, 2001).

To conclude, although the brain of a songbird differs significantly from ours and does not show the same architecture as a mammalian brain, similar neural mechanisms may drive the development, perception and production of learned vocalizations. Although the abovementioned parallels on the neural level all provide pieces to the puzzle, overarching theories, addressing the common neural basis of vocal learning, are still lacking. This thesis aims to contribute to the understanding of common neural mechanisms underlying vocal learning in songbirds and humans. In order to compare the neural mechanisms underlying both learning and perception of species-specific vocalizations, this thesis presents three functional Magnetic Resonance Imaging studies, addressing the neural substrate of (i) perception of learned vocalizations in adult songbirds (Chapter 3), (ii) birdsong learning within the sensitive period for vocal learning (Chapter 4) and (iii) human artificial grammar learning and perception of the learned grammar (Chapter 5). Additionally,

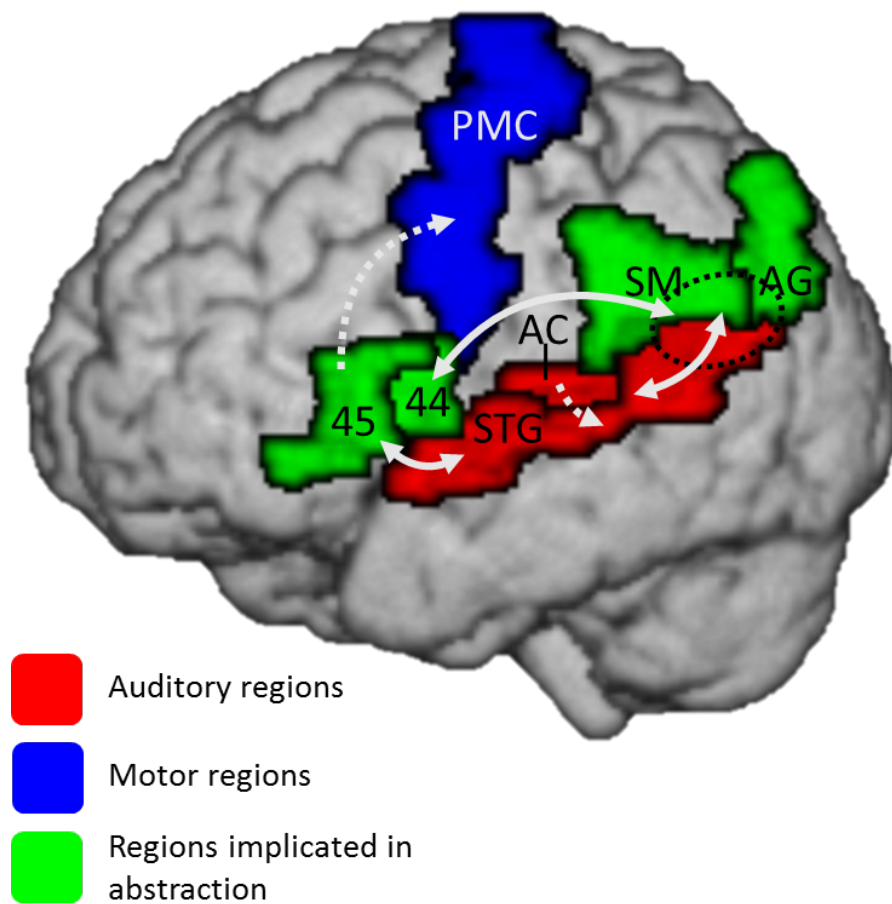


Figure 1.3: Human brain regions implicated in language processing. AC: Auditory Cortex, STG: Superior Temporal Gyrus, PMC: Primary Motor Cortex, 45: BA 45 or Pars Triangularis of the Inferior Frontal Gyrus, 44: BA 44 or Pars Opercularis of the Inferior Frontal Gyrus (BA 44 and 45 are part of Broca's area, which is implicated in syntactic processing), AG: Angular Gyrus, SM: Supramarginal Gyrus. The dotted oval shows the location of Wernicke's area, which is implicated in semantic processing.

the contribution of brain connectivity to learning new linguistic structures in addressed in Chapter 6.

1.2 fMRI for comparative studies on vocal learning

1.2.1 Methods for songbird and human brain research

Both on the behavioral and the neural level, parallels between birdsong and human language have been demonstrated (for a review, see Doupe & Kuhl, 1999). However, studying birds and humans often requires different methodologies which have traditionally been used in separate fields. Therefore, a large number of parallels have been drawn based on studies conducted in a single species. Recently, song and speech learning have been compared using similar behavioral methods (Gobes et al., 2009; Ter Haar, 2013), but no comparative studies addressing the neural correlates of birdsong learning and human language acquisition have been conducted to date.

Traditionally, studies addressing the neural substrates underlying birdsong learning have employed invasive methods such as electrophysiology and IEG expression (for a review see Bolhuis & Gahr, 2006). These types of studies have contributed greatly to our understanding of the neural substrates of birdsong learning and the song system. Moreover, they were the basis for a number of hypotheses about the cellular and molecular basis of human language acquisition (Doupe & Kuhl, 1999). However, these methods might not be best suited for comparative studies involving humans, because they focus on the cellular level, while the non-invasive methods typically applied in human research operate on the neuronal population level.

For example, electrophysiological research in non-human primates has led to the discovery of mirror neurons (Rizzolatti, Fadiga, Gallese, & Fogassi, 1996). Songbirds have also been shown to possess auditory forebrain neurons that are both activated during song production and listening to the same song (Prather, Peters, Nowicki, & Mooney, 2008). However, these studies used single-cell measurements, which cannot be employed in human participants, because this method is highly invasive. Human fMRI studies, on the other hand, cannot establish whether specific cells have true mirror neuron properties, although the hypothesized right-hemisphere human mirror neuron system shows striking similarities with left-hemisphere networks involved in human language processing and production (Iacoboni, 2005). In this case, songbirds can inform questions about the role of mirror neurons in vocal learning and the use of songbird (and primate) fMRI in combination with electrophysiology can aid the validation of human fMRI results.

Songbird studies aiming to understand vocal learning processes in humans search for common neural or genetic mechanisms to explain common behavior, but direct comparisons between the neural substrates of human language and birdsong development have yet to be made. In order to achieve

a sound comparison between species, ideally, the same experimental methods are used. Because studies of human brain function typically involve non-invasive (neuro-imaging) methods such as EEG or (functional) MRI, the Bio-Imaging Lab in Antwerp has taken the approach to implement fMRI in zebra finches (Boumans, Theunissen, Poirier, & Van der Linden, 2007). Because fMRI has also been established in non-human primates (Logothetis, Guggenberger, Peled, & Pauls, 1999), the neural correlates of vocal learning and memory can now be effectively compared between songbirds, non-human primates and humans. The studies described in the present thesis employ auditory fMRI in zebra finches and human subjects in order to uncover the neural substrates of auditory vocal learning in both species.

1.2.2 **fMRI in songbirds and humans**

Due to its non-invasiveness, using fMRI to study the neural correlates of bird-song learning has several advantages. Firstly, we can compare the development of the neural substrates for vocal learning in songbirds and humans. Secondly, because animals are not sacrificed after the experiment, longitudinal studies are possible and finally, the whole brain can be studied, which facilitates the study of large-scale brain changes. This technique thus enables us to longitudinally follow birdsong development in the same individuals and to consequently compare these data to fMRI data on human language development or auditory perception and memory in non-human primates.

In recent years, auditory fMRI in zebra finches has revealed highly specific responses to species-specific sounds (Boumans, Vignal, et al., 2008), the bird's own song (Poirier et al., 2009) and the song of the bird's father, which was learned during development (see Chapter 3 or Van der Kant et al. (2013)). Furthermore, the technique to acquire auditory fMRI data from juvenile zebra finches has been developed and applied for the first time for the research reported in the present thesis (see Chapter 4). These developments, as well as the technical details and challenges of songbird fMRI, are reviewed in Chapter 2.

Although the results are promising, there are still some limitations to interspecies comparative studies using (f)MRI. One of these limitations is the need for anesthesia when collecting fMRI data from small songbirds. Like humans, non-human primates like macaques (Petkov et al., 2006, 2008) as well as pigeons (De Groof et al., 2013) can be measured in an awake state, although a significant amount of training is needed. However, fMRI in awake zebra finches has yet to be established and the skittish nature of these small songbirds might complicate training. Furthermore, the extensive training periods required for awake animal fMRI experiments limit the possibilities for developmental studies. Anesthesia might also influence the BOLD response, which complicates the comparison with humans. Specifically, isoflurane, which is used for zebra finch fMRI studies described in this thesis, works through the GABA-ergic system and might thus influence responses in GABA-ergic neu-

rons. Indeed, in a number of brain regions, selective responses to the bird's own song appear to depend on cognitive state (Cardin & Schmidt, 2004; Dave, Albert, & Margoliash, 1998). Measuring songbirds under anesthesia also means that stimulation of the auditory system is not influenced by attention, which is the case in human fMRI studies.

Although anxiety is less of an issue in human subjects, including children (Westra et al., 2011), in The Netherlands, inclusion of children younger than eight years in MRI experiments without anesthetic in a non-clinical setting is not allowed (Central Committee on Research Involving Human Subjects, 2004). Therefore, fMRI experiments in children can only be conducted after the start of first language acquisition. Near InfraRed Spectroscopy (NIRS), like fMRI, is based upon a hemodynamic signal. This method is suitable for use in infants, even newborns (Gervain, Macagno, Cogoi, Peña, & Mehler, 2008), because the signal is obtained by measuring infrared light, scattered by the cortex, directly on the scalp. Because light is used and sources and detectors are placed directly on the scalp, this method does not involve a confined space, a magnetic field or radio-frequency pulses. However, the light does not penetrate very deep, limiting measurements to the outer layers of the cortex.

Not only the need for anesthesia, but also the nature of birdsong and human language pose challenges to comparative studies. The complexity of human language requires the isolation of a single aspect of language learning or speech perception in order to test specific predictions about this process. On the other hand, tasks can and need to be more challenging for humans and participants can be asked for behavioral responses, which allows for the testing of more intricate processes like grammar learning. Zebra finches only learn a single song, implying that all that has been learned can be tested in a single experiment. However, due to the anesthesia, behavioral responses cannot be obtained and the need for a social context excludes the possibility of tutoring a songbird in the scanner and observing the learning process.

These practical differences between human and songbird fMRI studies complicate the comparison between the BOLD responses. However, if the limitations are taken into consideration, human and songbird fMRI both provide information about the haemodynamic response to auditory stimulation with species-specific vocalizations that can be either learned or non-learned. Because the level at which the measurements are taken (larger groups of neurons) and the neural mechanism that is measured (the BOLD response) are the same, songbird and human fMRI studies provide a manner through which hypotheses regarding neural processes underlying vocal learning, stated based on previous behavioral and invasive studies, can be assessed using a comparative approach.

In the studies described in the present thesis, experimental conditions could not be kept exactly the same for human subjects and songbirds. In contrast to songbirds, human subjects cannot be isolated from species-specific vocalizations and thus will never enter into an fMRI experiment naive. Conse-

quently, studying the acquisition of elements from a known natural language is problematic.

In order to overcome the language experience that adult humans necessarily have, we employed artificial grammar learning to study language acquisition from mere exposure in adult humans. An artificial grammar was introduced to serve as a new language-like stimulus that could be learned in the course of an experiment and consequently tested. While the learning process and its outcomes in songbirds are studied in a juvenile and an adult group, in humans the process is simulated in a single group of adult subjects.

1.3 Research questions and hypothesis

In this introduction, the framework was outlined within which this thesis employs fMRI in both the songbird model and human artificial grammar learning to study the neural underpinnings of human language acquisition. Furthermore, some of the methodological challenges faced in comparative research studying both human and animal brains have been discussed. In the studies described in the experimental part of this thesis, fMRI in both songbirds and humans will be used to study the neural mechanisms underlying birdsong learning and human artificial grammar learning. In a series of fMRI studies investigating these neural mechanisms in adult and juvenile zebra finches and human adults, this thesis compares the neural substrates of song learning in birds with those of language learning in humans. With these studies, it aims to shed light on the following research questions:

1. To what extent do the neural substrates of birdsong learning and human language acquisition show similarities?
2. Can potential similarities be ascribed to common neurocognitive mechanisms underlying the development of both birdsong and human language?
3. Are our fMRI results able to strengthen the birdsong model with a brain-based account of the behavioral similarities found in songbirds and humans with regard to vocal learning?

We hypothesize that in both species, vocal learning will “tune” the brain towards a state where it shows selective responses to learned species-specific communication signals (e.g. a specific (artificial) grammar in humans or a specific song in birds). Therefore, a song or a grammar that was perceived before, specifically if it was learned within the sensitive period for song or language development, will elicit a larger activation in regions that are implicated in learning species-specific vocalizations. The development of selectivity for learned vocalizations might represent a common neural mechanism underlying vocal learning.

1.4 Contributions

Chapter 1: conception, literature study and paper and manuscript writing: Anne van der Kant

Chapter 2: conception: Annemie Van der Linden, paper writing: Lisbeth Van Ruijssevelt and Anne van der Kant, manuscript supervision: Geert De Groof and Annemie van der Linden

Chapter 3: conception and experimental design: Colline Poirier, bird rearing: Sébastien Derégnaucourt, data collection: Anne van der Kant, data analysis and paper writing: Anne van der Kant and Colline Poirier, manuscript supervision: Annemie Van der Linden and Manfred Gahr

Chapter 4: conception and experimental design: Anne van der Kant, bird rearing and data collection: Anne van der Kant, data analysis and paper writing: Anne van der Kant and Lisbeth Van Ruijssevelt

Chapter 5: conception and experimental design: Anne van der Kant, data collection: Anne van der Kant and Daan van de Velde, data analysis and manuscript writing: Anne van der Kant, manuscript supervision: Niels Schiller and Claartje Levelt

Chapter 6: conception and experimental design: Anne van der Kant, data collection: Anne van der Kant and Daan van de Velde, data analysis and manuscript writing: Anne van der Kant, manuscript supervision: Niels Schiller

Chapter 7: conception, literature study and manuscript writing: Anne van der Kant

