The flexible listener: exploring zebra finch sensitivity to spectral and temporal sound features
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General Introduction

Chapter 1

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In one of his monumental books, "The Descent of Man, and Selection in Relation to Sex", Charles Darwin (1871) wrote that "the difference in mind between man and the higher animals, great as it is, is certainly one of degree and not of kind". This perspective has served as a cornerstone in comprehending the intricate complexities of auditory perception. Darwin also noted: "The sounds uttered by birds offer in several respects the nearest analogy to language" (Darwin, 1871), referring to shared cognitive traits in communication among human beings and birds. Darwin's idea that bird vocalizations offer an analogy to human language was based on his keen observations of the complexity and functionality of bird songs, the adaptability and diversity in vocalizations, and the similarity between the process of birdsong acquisition and human language development through exposure and imitation. This assertion aligns with the historical understanding that many animals rely on conspecific vocal signals for communication, which have evolved to convey specific information essential for, among others, mate attraction, individual identification, and resource defence. Such vocal signals are processed through species-specific auditory systems, enabling organisms to actively seek meaningful and relevant information from their environment, as envisioned by the concept of the "Umwelt" (von Uexküll, 1992). Noticeably, while each species possesses its own specific "umwelt", there are also similarities in auditory perception between humans and non-human animals, even though the auditory capabilities of non-human animals may not fully equate to the auditory perceptual abilities as observed in the human recognition of acoustic variation in language or music.

Both vocal communications through language and music perception constitute two of the highest-level cognitive skills evident in humans. All humans (independent of their culture, region, preferences, etc), have a predisposition for music, just as we have for language. Historically, it is well known that many animals use vocal signals to communicate, some of which sound highly musical to humans (e.g., the sophisticated songs of humpback whales or melodious songs of songbirds). While animal vocalizations often share features of melodic and rhythmic characteristics of what we regard as *music*, it's not easy to infer that animals possess the capacity for music. A more informative strategy is to identify which of the traits that enable humans to make or appreciate music we share with other animals, i.e., to examine their musicality. Musicality can be defined as a natural, spontaneously developing set of traits based on and constrained by our cognitive abilities and their underlying biology (Honing *et al.*, 2015). Similar to the language faculty, the human music faculty encompasses a suite of perceptual and cognitive abilities, some shared with nonhuman animals and some distinctively human (reviewed by Honing *et al*., 2015). Given that some animal vocalizations, in particular bird songs, are also characterized by spectral and temporal complexity as well as rhythmic patterns, some constituent cognitive components of musicality, such as relative pitch, tonal encoding, beat perception, and metrical encoding of rhythm, may be shared between humans and other species (Hoeschele *et al*., 2015). The study of musicality transcends the debate regarding whether animal vocalizations should be considered music, language, or both. Instead, it focuses on understanding the perceptual and cognitive mechanisms used to interpret sounds that may be deemed *musical* or *linguistic*. Drawing inspiration from Darwin's insights that the distinctions in mental traits between humans and animals exist on a continuum rather than being absolute, these subcomponents may have diverse evolutionary histories, and similar components or precursors may hence be present in other species. Conducting comparative research has the potential to reveal such similarities and thus provide insights into the evolutionary background of human language and musicality. Therefore, studying the mechanisms underlying the auditory perception of songbirds from a comparative perspective will be a valuable contribution for revealing shared perceptual abilities across species and offers insights into the evolution of human language and musicality.

Avian Model for Auditory Research

Songbirds are one of the most relevant groups for comparative language and speech research. Like speech, birdsong is characterized by the rapid production of acoustically varying syllables. Unlike the vocalizations in many other groups of animals, bird songs are learned from a tutor and, when acquiring their song, many songbird species go through similar phases to human infants learning language (Doupe & Kuhl, 1999; Bolhuis *et al*., 2010). As a widely used model species, studies on the zebra finch provide valuable insights into the intricate processes of vocal learning (e.g., Arnold, 1975; Boehner, 1983; Clayton, 1988; Zann, 1990; Mello, 2014; Hyland Bruno *et al*., 2021), rhythm detection (e.g., Nagel *et al*., 2010; van der Aa *et al*., 2015; Benichov *et al*., 2016; ten Cate *et al*., 2016; Lampen *et al*., 2019; Rouse *et al*., 2021), and the processing of complexly structured auditory stimuli (e.g., Okanoya & Dooling, 1990a; Okanoya & Dooling, 1990b; Uno *et al*., 1997; Lohr & Dooling, 1998; Dent *et al*., 2008; Osmanski *et al*., 2009; van Heijningen *et al*., 2009; Spierings & ten Cate, 2014; Spierings & ten Cate, 2016; Chen *et al*., 2016; Spierings *et al*., 2017). Like other social songbirds, zebra finches employ a diverse range of vocalizations, including song and other types, to communicate with conspecifics, with songs being particularly noteworthy for their acoustic complexity and consistent imitation within their vocal repertoire (Elie & Theunissen, 2020). A quantitative analysis of the zebra finch's complete vocal repertoire (Elie & Theunissen, 2016) revealed that vocalization types are primarily categorized based on the shape of the spectral envelope, attributed to formants produced by the syrinx and vocal tract, indicating that dynamic vocal tract shaping is not unique to humans or a few mammals. Zebra finch vocalization types were found to exhibit distinctions in spectral shape, pitch saliency, duration, and intensity, with their spectral shape primarily distinguishing vocalizations in various behavioural contexts, and pitch saliency further differentiating noisy calls from tonal or harmonic sounds (Elie & Theunissen, 2016). Surprisingly, despite being more distantly related to humans than other mammals, songbirds, including zebra finches, share striking similarities with humans in their perception of these acoustic features (ten Cate, 2018). Utilizing this model species in investigating both spectral and temporal features in auditory stimulus processing hence has the potential to significantly contribute to current theories regarding the biological foundations and origins of human speech processing and musicality, particularly in relation to spectral and rhythm perception. This kind of research aligns with the broader focus of comparative research in this context, which has primarily centred on songbirds' perception of two crucial aspects: spectral attributes (e.g., pitch, timbre/harmonics) and temporal attributes (e.g., tempo/rhythm).

Perception of Pitch & Spectral Attributes

Humans and birds share interesting similarities with regard to their auditory processing (Hoeschele, 2017). For example, humans and European starlings have similar frequency sensitivity, can perceive the pitch of the missing fundamental, and parse multiple pure-tone sequences into separate auditory streams (e.g., Hulse *et al.*, 1984; Hoeschele, 2017). Given these similarities, it is surprising to find a major difference in how humans and birds perceive sequences of tones. Humans readily recognize tone sequences that are shifted up or down in log frequency because the pattern of relative pitches is maintained (referred to as relative pitch). In contrast, birds were assumed to have a strong bias to rely on the absolute pitch for the recognition of tone sequences - a pitch-shifted melody seems to be perceived as an altogether different melody (Hulse *et al.*, 1984). However, starlings can maintain the discrimination between two songs shifted in frequency (Bregman *et al*., 2012). It is unclear what causes this difference in responses between shifts in artificial tone sequences and in songs. Bregman *et al*., (2016) propose that the perception of melodic sequences in songbirds relies on a perceptual representation that appears more closely tied to the spectral envelope rather than absolute pitch cues. Starlings, for instance, rely mainly on a perception of each tone based on its spectral envelope (the shape of the spectrum, formed by the relative amplitudes of the different frequency components) rather than abstracted features derived from the fundamental frequency (absolute pitch) or on the relative power in the harmonics (timbre) (Bregman *et al*., 2016). This led to the hypothesis (Bregman *et al*., 2016) that the spectral envelope governs avian tone sequence recognition: for pure tones, the spectral band envelope corresponds directly to pitch; for complex tones, the spectral band envelope contributes to both pitch and timbre perceptions. Noticeably, spectral envelope is not the only attribute that the birds attend to in auditory discrimination. A previous study from our own lab showed that zebra finches can discriminate artificial vowel-like elements differing in pitch and harmonic spectrum using either of these while ignoring the other, and it also showed that zebra finches can generalize a harmonic spectrum to a vocoded version (Burgering *et al*., 2018). The findings of Burgering *et al*. (2019) and Bregman *et al*. (2016) suggest that while zebra finches demonstrate a capacity to detect pitch variations in songs, this sensitivity may not necessarily reflect an inherent pitch sensitivity but rather could be attributed to their sensitivity to the spectral envelope. Notably, this aspect has so far not been examined specifically in the context of song stimuli. Therefore, the perception of pitch and spectral attributes by zebra finches is one of the central topics addressed in this thesis.

Beat Detection & Perception of Temporal Regularities

Humans can easily detect the beat in music, perceive regularity in a series of pulses, and recognize melodies as being similar despite differences in the speed of performance. Although it was assumed that animals had similar abilities (Darwin, 1871), this has long remained untested. The question of whether animals can detect regularity in a stimulus got sudden attention with the discovery of Snowball, a Sulphur-crested cockatoo (*Cacatua galerita*) that could entrain head and body movements with the beat of several popular songs (Patel *et al*., 2009). Parrots, such as Snowball, are vocal learners, and vocal learning is associated with evolutionary modifications to the basal ganglia, which play a key role in mediating a link between auditory input and motor output during learning (Petkov & Jarvis, 2014). However, other studies have revealed that this issue is also one with many open questions and have questioned the link between vocal learning and beat perception (ten Cate *et al*., 2016; Wilson & Cook, 2016; Celma-Miralles & Toro, 2020). They suggest the presence of a graded scale for beat perception in avian species (ten Cate *et al*., 2016), with some species (including the zebra finch) attending more strongly to local features of the individual stimuli rather than the overall regularity of the stimuli (which is a main feature human listeners attend to, e.g., van der Aa *et al*, 2015).

The perception of temporal regularity is one of the basic features of musicality. Yet, the current evidence for detecting pattern regularities in zebra finches seems ambiguous: a study using single-tone pulse strings as rhythmic stimuli showed that discrimination between isochronous and heterochronous stimuli disappeared with a 25% tempo change (van der Aa *et al*, 2015), and another study using more complex two-tone pulse strings as rhythmic stimuli found that some discrimination was maintained with a 25% shortening, but not with a 25% lengthening of element and pause durations (ten Cate *et al*., 2016). In contrast to this sensitivity to tempo in tonal strings, zebra finches showed great tolerance for changes in song duration (61%~164%) in a song discrimination study by Nagel *et al*. (2010). The results of van der Aa *et al*. (2015) suggest the birds attended only to local temporal features (e.g., the exact duration of inter-onset intervals). By contrast, those of Nagel *et al*. (2010) indicate that birds do attend to somewhat global rhythmic features and might have used predominantly frequency or intensity cues during song categorization. The local feature bias hypothesis (ten Cate *et al*., 2016) might provide a framework to interpret the discrepancies among those studies, which suggests a preference in birds for local temporal features in perception and discrimination tasks with simple stimuli and a lower sensitivity when these features are part of a spectrally more complex structure.

Cognitive Flexibility?

A possible explanation for the, at times, contradictory findings in avian cognition concerning the relevance of various spectral and temporal features for auditory discrimination might be the presence of cognitive flexibility. This cognitive flexibility involves the mental ability to adapt to changing conditions, switch between different tasks, or adjust one's strategies in response to new information. Zebra finches appear to demonstrate this flexibility in their perceptual strategy, as demonstrated in the study by Burgering *et al*. (2018), where they could use either the pitch or the spectral envelope, depending on which is most relevant to succeed in the auditory task. What the different studies suggest is that birds can use pitch or other spectral features of acoustic stimuli (e.g., formant, spectral envelope, spectral centroid, etc.) to identify different stimuli. Despite the insights from Burgering *et al*. (2018), no study has systematically investigated how zebra finches invoke pitch or other spectral attributes, such as harmonicity,, spectral envelope, or other relevant spectral features, to differentiate between two tonal sequences or conspecific vocalizations in which these attributes have been manipulated In addition to the perceptual flexibility (i.e., the ability to perceive and interpret information from the environment in a flexible manner, including the capacity to attend to and process different sensory cues or modalities) that zebra finches demonstrate for spectral features, the apparently contradictory findings regarding the sensitivity to temporal features might also be explained by similar flexibility in songbirds' attention to various temporal features.

An open question is whether, and to what extent, the birds' attention to spectral attributes/features and temporal parameters/patterns depends on the differences between the training stimuli. If zebra finches can flexibly adjust their perceptual strategies to accommodate varying parameters or patterns in auditory stimuli, how do these parameters or patterns relate to each other? And are there biases in the attention and preference among zebra finches in employing cues such as spectro-temporal fine structure, temporal pattern, and spectral structure? Additionally, the presence of a graded scale for beat perception in avian species (ten Cate *et al*., 2016) may indicate that the spectrally rich structure of songs, containing modulations of pitch and spectral contour, may interact with (or overshadow) the attention given to temporal changes. So, as for the perception in the frequency domain, a critical question for experimental studies on the interplay of spectral and temporal perception in zebra finches is how the nature of the stimuli affects the birds' discrimination. This focus leads to questions regarding how the perception of auditory stimuli is affected by stimulus complexity. This thesis has the ambition to fill critical gaps in our understanding of songbird auditory cognition by investigating the role of spectral and temporal features in zebra finches' discrimination of songs and other tonal sequences and spectrally complex stimuli. The research is expected to be useful for understanding the interplay between various spectral and temporal features in songbirds' auditory perception and to provide insights into the adaptability of songbirds' perceptual strategies across diverse acoustic contexts.

Thesis Outline

This thesis consists of 4 chapters of empirical research, addressing questions from song discrimination and song preferences to the perceptual interplay of specific acoustic features/patterns. These questions were addressed by using a well-established experimental paradigm, the Go-left/Go-right operant task, which was employed across three experimental chapters (**Chapter 2**, **Chapter 4**, and **Chapter 5**) to investigate the cues utilized by birds in discriminating natural songs and artificial stimuli. In this task, the birds have to learn to peck a central sensor to trigger a sound and then choose either the left or right sensor, with correct choices rewarded with food and incorrect ones resulting in a brief light-off as negative feedback. The birds are initially trained to discriminate between a pair of sounds without any constraints on the cues used for identification. Subsequently, they are tested with novel probe stimuli in which specific cues have been altered. Importantly, probe stimuli are presented without any reinforcement linked to the bird's choice, thus preventing the bird from learning a predetermined "correct" response through the reward/punishment pattern. Successful discrimination between probe stimuli derived from different training stimuli, with performance significantly above chance, serves as evidence of the bird's ability to recognize a modified version as being derived from a specific training stimulus. By offering sets of acoustic stimuli and letting the bird choose which to attend, this methodology enables the determination of the features that birds use to identify complex stimuli within a given context. Notably, this paradigm facilitates the presentation of multiple test stimuli within a short time frame during the test phase, can be applied to both male and female birds using a uniform approach, and allows for a clear distinction between incorrect responses (choosing the wrong answer), which may indicate that a test stimulus has modified a song feature in such a way that it now resembles the opposite training stimulus more than the original one or a failure to discriminate the probe sound, and a simple lack of response (no response), which could suggest factors such as confusion, fatigue, indifference, or inattention. **Chapter 3**, serving as a supplementary preference assessment following the operant task in **Chapter 2**, focuses on comparing the preferences for heterospecific songs and modified conspecific songs with those for natural conspecific songs.

Chapter 2 explores how zebra finches attend to spectral and temporal variation in recognizing conspecific song motifs. This chapter systematically examines the importance of spectral and temporal parameters when zebra finches have to discriminate two natural songs, which are either similar or different in their duration. Moreover, this chapter discusses the results from a discrimination task using an operant conditioning paradigm (the Go-left/Go-right task) in which birds are trained to respond to one type of sound for a food or water reward and to not, or to respond differently to another sound, with errors resulting in consequences such as brief periods of darkness or no reward, examining which sound features birds use for discrimination. The controlled experiment examined how the difference in song duration affects how zebra finches perceive and discriminate natural motifs of their conspecific songs, their noise-vocoded version in which the pitch was removed but the spectral envelope was maintained, as well as other modified versions varying in spectral (pitch, or frequency spectrum) and temporal features (duration/tempo). Through a comprehensive analysis, this chapter elucidates the types of parameters birds can leverage and hence the information that birds may extract from vocalization.

Chapter 3 examines the song preferences exhibited by both male and female zebra finches. Building upon the findings of **Chapter 2**, which explored the birds' perceptual sensitivity to various acoustic features in an operant discrimination task, **Chapter 3** deals with the question: does the low response rate to specific novel stimuli in the discrimination tasks arise from these stimuli being perceived as too different from the training songs or from a very low attractiveness of these stimuli? To investigate this, a 4-way operant choice test (referred to as the "carrousel") was used to measure birds' preferences. In this setup, birds could perch on different operant perches within the carrousel setup, thereby triggering the playback of four different songs. This chapter explores the birds' preference for different song types, including normal, duration-stretched, and vocoded conspecific songs, as well as heterospecific songs. This chapter also examines the presence or absence of a sex difference in song preference.

Chapter 4 addresses the question of how learning about the spectro-temporal structure and sequential order of song syllables relate to each other. The Go-left/Go-right task was once again used in this chapter to directly compare the birds' relative sensitivity to attend to spectro-temporal features and syllable sequence for song discrimination. Birds were either trained to discriminate between two song-syllable strings that consisted of identical syllables or trained to discriminate between two strings containing different syllables. This chapter examines whether zebra finches exhibit cognitive flexibility in their ability to attend to sequential and spectro-temporal features, depending on the salience of the differences between two auditory stimulus strings during discrimination learning.

Chapter 5 examines the zebra finches' sensitivity to pitch and formant patterns, two fundamental features crucial for human speech recognition and musical perception. It examines whether there is an interplay between pitch and formant when both vary between stimuli and which of these two spectral parameters is most salient to zebra finches. To investigate this, the stimuli used in this chapter were sound sequences consisting of five artificial elements, separated by brief pauses. These artificial elements featured either simultaneous pitch and formant contour ascending and descending in the same direction over a full sequence or opposite directions over a full sequence. By employing the Go-left/Go-right paradigm once more, this chapter examined which of these two spectral attributes is more important in recognition of artificial tone sequences and whether the way in which pitch and formant are combined in the training stimuli affects the ease of learning and discrimination of the test stimuli.

Chapter 6 contains a synthesis of the findings obtained across the four experimental chapters. It summarizes the findings of the previous chapters and, discusses them, offering overarching conclusions regarding the diverse cues involved in songbirds' auditory perception. Collectively, these findings offer a comprehensive perspective on auditory cognition in zebra finches. This chapter delves into the broader implications of the main conclusions of the thesis and explores how this research enhances our understanding of songbirds' perceptual flexibility with respect to the effect of the training context. Furthermore, this concluding chapter highlights potential research directions for future studies concerning the cognitive flexibility of songbirds.

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