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

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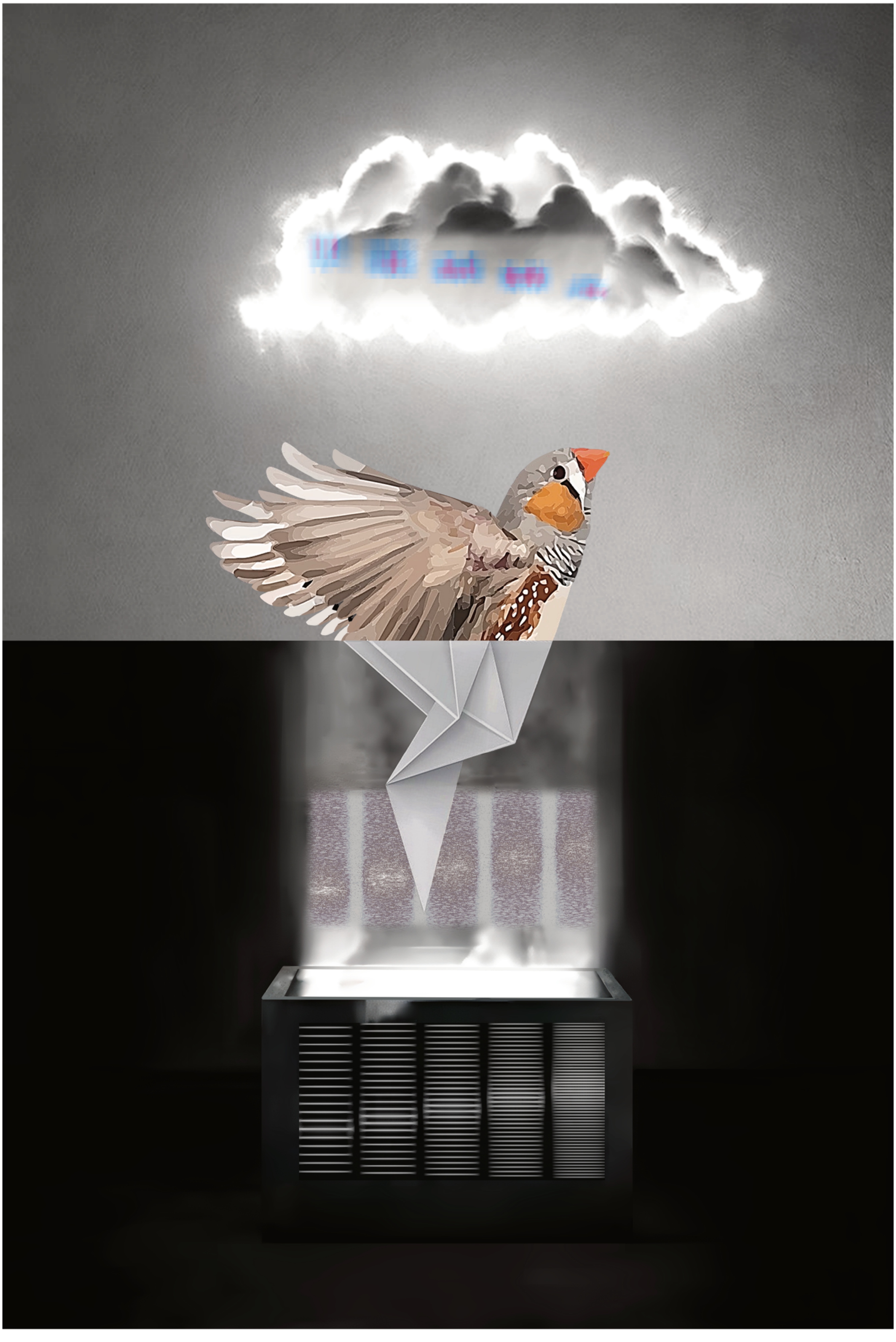

General Summary, Discussion & Conclusion

Chapter 6

Chapter 6

Summary of Findings from Different Chapters

Chapter 2 investigated the role of spectral characteristics and absolute duration of songs in zebra finch song recognition. The results indicated that zebra finches can attend to both spectral features and song duration in discriminating between two songs, and the relative salience of these acoustic parameters varies depending on whether these songs differ in absolute song duration or not in the training phase. Interestingly, when song duration serves as an additional distinguishing cue in song discrimination, spectral features play a less prominent role. In this chapter, I demonstrate that the acoustic features to which zebra finches attend when identifying or discriminating their conspecific songs may not be as fixed as previously assumed. Instead, their focus on these features appears to be influenced by the characteristics of the stimuli. This observed flexibility in auditory processing, coupled with the potential importance of variations in song duration for song perception, calls for systematic research into the acoustic parameters that zebra finches may utilize in the perception of their conspecific songs.

Chapter 3 expanded upon these insights by exploring the preferences of female and male zebra finches for normal and modified songs. By comparing the count of perch visits by which the birds could expose themselves to different stimuli among different sex groups, the study reveals an intriguing pattern: Females displayed a preference gradient, preferring normal and duration-stretched conspecific songs over vocoded versions, but still preferring vocoded conspecific songs over heterospecific great tit songs. In contrast, males only preferred duration-stretched conspecific songs over heterospecific songs and showed limited differentiation in their preference among the stimuli. In addition, female zebra finches display significantly greater activity in this task, underscoring the more pronounced song preferences observed in females compared to their male counterparts. Interestingly, while altering song duration did affect song discrimination in the operant discrimination task (Chapter 2), it did not significantly influence song preference in Chapter 3. As no sex difference was present in the discrimination studies in chapter 2, this chapter thus highlights that the attendance to, and importance of, various acoustic parameters is both task and sex dependent. It underscores the importance of employing multiple approaches and testing paradigms to avoid potential blind spots inherent in a single experimental paradigm.

Chapter 4 delved into the cognitive flexibility of zebra finches in using phonology and the sequence of syllables for auditory discrimination. Birds trained to discriminate between two song-syllable strings that consisted of identical syllables took an equal number of training trials to birds trained on strings containing different syllables. Test trials showed that birds trained on strings with identical syllables had learned sequential cues in addition to spectro-temporal ones. This outcome confirmed the cognitive flexibility of zebra finches, indicating their perceptual attention to the song features that offer the most prominent distinctions between two syllable strings, be it spectro-temporal or sequential. It demonstrates that the role of phonological and sequential features in zebra finches' song recognition depends on the degree of song differences in these features.

Chapter 5 investigated the interplay of pitch and formant contours in melody recognition by zebra finches. It explored how zebra finches perceive and recognize tonal strings with varying pitch and formant attributes, either simultaneously ascending or descending in the same direction or opposite directions over a full string. The results revealed that zebra finches possess remarkable sensitivity to both pitch and formant attributes, enabling them to detect variations in pitch and formant contours across harmonic elements. Interestingly, the impact of pitch and formant is almost identical for both training conditions, which might suggest no or limited interaction between the two attributes when learning to discriminate the different tonal strings. In culmination with the insights from previous chapters, Chapter 5 provides thus further evidence of the zebra finches' ability to attend to various acoustic parameters, not only in response to stimuli consisting of natural song elements but also in the context of artificial tonal stimuli.

Below I synthesize the findings from the preceding four chapters and discuss the details and broader context of auditory cognition. First, I discuss zebra finches' perceptual flexibility, their sensitivity to acoustic features in different contexts, and their ability to focus on global as well as local features. Next, I explore how the nature of stimuli impacts sound discrimination, comparing natural and artificial sounds' effects on zebra finches and starlings. After this, I investigate the influence of the training context on zebra finches' perceptual flexibility, particularly regarding spectral and temporal features in song discrimination. Subsequently, I discuss auditory perception and discrimination variations between zebra finches and starlings, comparing their responses to vocoded stimuli, spectral features, and sensitivity to noise disruptions in harmonic structures, emphasizing potential interspecies differences. I then propose that these findings on the context-dependent perceptual flexibility of zebra finches add to the zebra finch's significance as a model for auditory research. Lastly, I suggest future research directions, focusing on uncovering cognitive mechanisms of perceptual flexibility and advocating for cross-species comparative studies in this field.

Perceptual Flexibility of Zebra Finches

One overarching theme that emerges from the experimental chapters is the remarkable perceptual flexibility of zebra finches. Previous studies have demonstrated that zebra finches can perceive a range of acoustic features (e.g., Uno *et al*., 1997; Lohr & Dooling, 1998; Dooling *et al*., 2002; Lohr *et al*., 2006; Nagel *et al*., 2010; Vernaleo *et al*., 2010; Vernaleo & Dooling, 2011; Vignal & Mathevon, 2011; Lawson *et al*., 2018; Prior *et al*., 2018a; Prior *et al*., 2018b; Geberzahn & Derégnaucourt, 2020; Fishbein *et al*. 2021; Mol *et al*., 2021). However, while these studies revealed that zebra finches are capable of attending to various features, they generally did not investigate to what extent the choice of stimuli influenced the features to which they attended.

My findings suggest the perceptual flexibility of zebra finches in attending to either spectral features or duration of songs (Chapter 2) and to either spectral structure or sequence of syllables (Chapter 4) depending on the training context (i.e., the salient differences in sound features between the training stimuli). This observation aligns with the results of a study by Burgering *et al*. (2019), which demonstrated that zebra finches can use either pitch or spectral envelope as cues in discriminating vowel-like sounds, depending on the salient differences between the stimuli. This flexibility is also supported by behavioural evidence, such as a Go-Nogo operant task, where zebra finches were observed attending to specific features when differentiating between harmonic sounds (Uno *et al*., 1997). In Uno *et al*.' study (1997), when the only difference between two harmonic sounds was the second harmonic, zebra finches focused on this feature. Moreover, some zebra finches tended to rely on the fundamental frequency as a discriminative cue when the number of harmonics was limited. These results underline the zebra finches' ability to adapt perceptual strategies based on the contrasts between the stimuli they need to differentiate. My findings, along with those from other studies mentioned above, contribute to the understanding of perceptual flexibility in zebra finches' auditory processing, as different features appeared to be relevant in various contexts.

Moreover, the findings reveal that zebra finches' attention is not limited to spectral features but also extends to temporal features. These birds demonstrate a sensitivity to both local features, such as the spectro-temporal fine structure of syllables, and global features, including the sequential order of syllables within a song. The perceptual flexibility for global features is particularly evident in Chapter 4, where zebra finches showcased their ability to adapt and discriminate songs based on phonological and sequential aspects. This demonstrates their capacity to process and utilize the overall structure of songs rather than merely focusing on individual elements.

The observed perceptual flexibility enables birds to adapt their perceptual tuning to the most relevant acoustic dimensions for distinguishing between songs of different individuals or other biologically relevant sounds. It's likely that the zebra finch is not the unique species exhibiting this cognitive ability, though further crossed-species research is needed to confirm this. Also, many neurobiological studies on auditory perception in songbirds often treat perceptual sensitivities as static (e.g., Theunissen & Doupe, 1998; Sen *et al.*, 2001; Meliza & Margoliash, 2012; Cazala *et al.*, 2019; Inda *et al.*, 2021). Our study suggests that researchers should consider the possibility that these sensitivities may vary based on the context (such as discriminating songs of different colony members or expressing a social or sexual preference) or the nature of the variation between the available stimuli. Investigating the regulation of this flexibility and identifying the brain areas crucial for specific contexts or tasks could be an intriguing topic for future neurobiological research.

Nature of Stimuli & Impact on Discrimination

Songbirds 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.*, 1984a). While it's commonly believed that songbirds primarily recognize tonal sounds based on absolute pitch rather than relative pitch (e.g., Weisman *et al.*, 2004; Hoeschele *et al.*, 2012b, 2013, 2014), it is interesting to note that starlings (Cynx *et al.*, 1986; Braaten *et al.*, 1990) and other songbirds (Hulse & Cynx, 1985; Hulse *et al.*, 1992) did exhibit some degree of perceptual sensitivity for relative pitch. When these birds were tested with artificial stimuli, they could only transfer their discrimination abilities between different tone sequences to novel patterns within the range of frequencies used to construct the patterns they initially learned to discriminate (Page *et al.*, 1989). However, starlings can maintain the discrimination between two songs shifted in frequency (Bregman *et al.*, 2012). Some other songbirds, like the white-throated sparrow (Hurly *et al.*, 1990) and black-capped chickadee (Weisman & Ratcliffe, 1989; Hoeschele *et al.*, 2012a), were also found to be sensitive to the relative pitch features in conspecific song. It is still unclear what causes this difference in responses between shifts in artificial tone sequences and in conspecific songs. A possible explanation is that the nature of the training stimuli impacts the birds' attention to specific acoustic features during discrimination tasks and the subsequent generalization of their learning to novel stimuli. This stimulus-dependent sensitivity in zebra finches and other songbirds implies that perceptual flexibility in sound discrimination may also be expected to exist across songbird species.

Equally noteworthy is the influence of the stimulus nature on the perceptual salience of different acoustic features that zebra finches may prioritize. Given the paramount role of song learning in zebra finches, encompassing abilities such as individual identification, mate attraction, rival repulsion, and the discrimination between conspecific and heterospecific songs, one would expect these birds to focus on a spectrum of acoustic parameters, including temporal aspects (e.g., duration), source-related characteristics (F0-based pitch), and filter-related attributes (such as formants) inherent in their conspecific songs. While one of our chapters delved into artificial stimuli, specifically tonal strings featuring pitch and formant contours (Chapter 5), others focused their investigations on conspecific songs (Chapter 2 and Chapter 4).

Patel (2017) suggested a hierarchy of cues for tone sequence recognition in songbirds, emphasizing spectral shape as a primary feature and pitch saliency as a significant secondary feature distinguishing tonal from noisy sounds. According to this, pitch perception might be a vital cue in distinguishing call types based on pitch saliency, especially if harmonic tones are less acoustically complex than real musical instrument sounds or if the spectral structure of complex harmonic tones remains consistent across tones (e.g., Bregman *et al.*, 2012). Surprisingly, while starlings are capable of relational processing (which entails the cognitive analysis of relationships, patterns, or dependencies among various features of a specific acoustic attribute within a given auditory context, emphasizing the interaction and contribution of its components to the overall perception of sound) for acoustic parameters like loudness (Bernard & Hulse, 1992) and rhythm (Hulse *et al.*, 1984b) in tone sequences, they do not exhibit the same ability for relational pitch processing. This implies that relative pitch may carry less weight than other parameters such as loudness and rhythm if a strict "hierarchy of cues" (as proposed by Patel, 2017) is employed by songbirds for sound recognition. However, it's worth noting that Patel also acknowledged that this hierarchy is not absolute and may vary depending on the complexity of the acoustic stimuli. In fact, my findings align with this notion that these distinct strategies might result from specific biases — in this context, the term "biases" is more precise than "hierarchy" — reflecting the weight or priority that certain birds give to certain features of an acoustic signals.

Perceptual flexibility emphasizes the adaptability of sensitivities to various acoustic features or perceptual attributes. The interplay between the nature of the training stimuli and the birds' sensitivity to specific acoustic features during discrimination tasks can lead to a more nuanced understanding of sound perception in songbirds. This suggests that while certain acoustic features or perceptual attributes, such as pitch, may play a crucial role in song discrimination, the flexibility and adaptability of these birds' perceptual systems are influenced by the context and stimuli they encounter during training and testing. Therefore, it's essential to consider the context-dependent nature of their cognitive processes in auditory discrimination research.

Impact of Training Context

The findings of this research highlight the value of the training context in modulating the perceptual flexibility of zebra finches. As elucidated in Chapter 2 and Chapter 4, the training context plays a pivotal role in determining the extent to which zebra finches rely on spectral and temporal features for discriminating songs. This highlights the need to account for training conditions when interpreting their auditory discrimination capabilities. Furthermore, Chapter 5 investigates whether the relative influence of pitch and formant in discriminating tone sequences differs depending on whether they change in the same or opposite directions across the sequences. Unlike the findings from Chapter 2 and Chapter 4, where conspecific sounds were used, Chapter 5 employed two distinct artificial stimulus sets. Remarkably, the result in Chapter 5 does not significantly vary with changes in the training context regardless of whether formant and pitch changes were congruent or opposite suggesting that both attributes are important but don't seem to interact with each other. Hence, the training context is clearly influential, but it's not the determining factor.

Sexual Bias on Song Preferences, as well as Song Discrimination?

The zebra finches display perceptual flexibility in song discrimination, yet they still have preferred song features they focus on. The research of Chapter 3 added another dimension to song discrimination by investigating potential sexual biases in song preferences. Chapter 3 brought to light that both female and male zebra finches exhibited preferences for duration-stretched conspecific songs over heterospecific songs, with females showing a gradient of preferences on the four song types (normal, duration-stretched, vocoded conspecific songs, and heterospecific songs) and displaying more pronounced preferences than males. The preference for conspecific songs over heterospecific ones in zebra finches is not surprising, as it has been supported by both behavioural and neural experimental evidence (Stenstrom *et al.*, 2022).

These findings prompt consideration of the distinct questions addressed by the two experimental paradigms and their respective limitations. Discrimination tasks primarily assess a songbird's ability to differentiate and recognize specific auditory cues, while preference tests focus on the bird's behavioural responses and subjective preferences for auditory stimuli. Comparing the results of both paradigms using the same stimulus set contributes to a more comprehensive understanding of songbirds' auditory perception of specific stimuli. However, it is worth noting that our results did not reveal any sexual differences in discrimination tasks, as evidenced in Chapter 2, Chapter 4, and Chapter 5. This suggests that the sexual biases observed in preference tests might be absent or comparatively subtle when birds are subjected to training and testing within the operant discrimination paradigm. This disparity implies that the specific experimental paradigm employed could influence the extent to which sexual differences are discernible. Furthermore, the variation in results between preference tests and discrimination tasks is not due to preference tests being more sensitive to sexual biases, but rather because these two experimental paradigms measure different cognitive traits. Moreover, the synthesis of these findings underscores the divergence in cognitive processes underpinning song preferences and auditory discrimination. This highlights the importance of tailoring the choice of a behavioural paradigm based on its specific focus on distinct cognitive functions.

Do Zebra Finches Attend to the Same Features as Starlings Do in Sound Discrimination?

The results from Chapter 2 of this thesis and those presented by Nagel *et al.* (2010) indicate that zebra finches are more sensitive to pitch changes (in the sense that pitch-shifted versions are considered different) of songs than starlings are, which can still show discrimination of songs with pitch shifts up to ±40% (Bregman *et al.*, 2012). Moreover, starlings appear to exhibit a greater inclination to focus on specific spectral features compared to zebra finches, which seem to attend to a wider variety of features. A comparable pattern emerges concerning specific features in starlings' attention to temporal characteristics. Starlings were more sensitive to changes in tone length (i.e., sound duration) than changes in the inter-onset interval (Hulse *et al.*, 1984b), while zebra finches appeared to assign equal importance to both temporal aspects (ten Cate *et al.*, 2016).

The findings in this thesis with regard to how zebra finches process vocoded stimuli, including conspecific songs and artificial tones, differ from earlier studies with starlings. Bregman *et al.* (2016) demonstrated that when presenting starlings with vocoded versions of sequences of tones (varying pitch and timbre), they maintained discrimination between these sequences. However, pitch-shifted versions did not, indicating that spectral envelope rather than pitch was used for discrimination by starlings. While Patel (2017) suggested that this might be a common strategy among birds, the reduced discrimination of noise-vocoded songs in zebra finches in my studies (Chapter 2 and Chapter 4) was surprisingly not in line with the studies on starlings' discrimination of artificial tone sequences. Even when tested with artificial tone stimuli (Chapter 5), zebra finches from both training conditions responded the least to the vocoded version among the five modified versions. The finding that zebra finches hardly discriminate noise-vocoded stimuli, whether they are conspecific songs or artificial sounds, suggests a distinction between songbird species in perceptual strategies regarding the utilization of spectral envelope in sound discrimination.

However, Burgering *et al.*'s study (2019) found support for the idea that zebra finches use spectral envelope for discriminating vowel-like sounds. The effectiveness of the stimulation of zebra finches' calls does not appear to rely on their fine acoustic structure, as these calls still evoke a strong behavioural response even when their acoustic features have been significantly modified (Vignal & Mathevon, 2011). This might suggest that spectral envelope is important for discriminating among calls or other shorter sounds, whereas discriminating songs relies more on attending to other spectral features, including pitch and harmonics, which has been demonstrated in various studies (e.g., Okanoya & Dooling, 1990; Uno *et al.*, 1997; Dooling & Lohr, 2006; Lohr *et al.*, 2006; Vignal & Mathevon, 2011; Prior *et al.*, 2018a; Prior *et al.*, 2018b).

In my experiments, the vocoded version proved to be the most easily detected as differing from the training sounds when compared to other stimulus modifications. This may be due to the fact that noise-vocoding disrupts not only pitch and the harmonic attributes of songs and sequence of tones but also introduces a but also introduces a noise-like, non-harmonic spectrum into the stimulus. These alterations, apparently, make the vocoded versions perceptually distinct from the training stimuli. Nonetheless, the zebra finches might still be capable of using spectral envelope as an acoustic cue in sound discrimination (supported by discrimination above chance in some cases of Chapter 4 and Chapter 5). If this is indeed the case, it suggests that zebra finches are more sensitive to the disruption of pitch and harmonic structures than starlings are. However, so far, there have been no studies examining how starlings respond to vocoded versions of natural songs (the stimuli Bregman *et al.* (2016) used were artificially synthesized sounds), leaving it to be explored whether such a stimulus would yield similar outcomes compared to testing with artificial sounds.

Lastly, more research is needed to test these claims more generally across avian species. Future research should explore cognitive flexibility in a broader range of avian species, including both songbirds and non-songbirds, using identical experimental paradigms and stimuli. This will aid in identifying the neural, ecological, and evolutionary factors associated with the cognitive flexibility.

An Ideal Avian Model for Auditory Research

This thesis has contributed to establishing the zebra finch as an avian model for research on auditory perception and processing, further contributing to the value attributed to these birds in the field of comparative cognition research. Their extensively studied neurobiological and behavioural characteristics, along with the observed perceptual flexibility in auditory discrimination, emphasize their significance as model species for understanding auditory processing in comparative studies. By using this avian model, I presented insights into the auditory abilities of zebra finches, showcasing their perceptual flexibility across spectral, temporal, and sequential attributes. It is evident that the birds' auditory sensitivity extends beyond the realm of local features, such as the fine-grained spectro-temporal structure of individual syllables, to encompass the ability to attend to global features, including the sequential order of syllables. Most notably, this sensitivity for global features is demonstrated when the birds successfully discriminate between two artificial tonal strings based on pitch contour and formant contour (as unveiled in Chapter 4). The notion of context-dependent cognitive flexibility and these birds' sensitivity beyond local features together suggest that there may still be other unexplored cognitive traits within this avian model.

Open Questions of Songbird Auditory Perception & Avenues for Future Research

While this thesis has yielded valuable insights into zebra finches' auditory perception, there remain open questions that elude our understanding. For example, further exploration is still needed to determine whether and how the interplay among various acoustic attributes impacts cognitive flexibility in avian auditory perception, and how these impacts depend on stimulus nature and ecological context. Additionally, there is still a lack of studies investigating which other species exhibit similar or contrasting levels of cognitive flexibility in auditory perception. As I conclude this study, it is imperative to delineate promising avenues for future research, capitalizing on the knowledge gleaned from our findings.

Future research endeavours should set their sights on unravelling the neural mechanisms that underpin the observed perceptual flexibility in zebra finches. Furthermore, delving into cross-species comparisons holds the promise of providing a broader perspective on auditory cognition (e.g., the impact of vocal learning on perceptual flexibility). Such comparative studies, encompassing both songbirds and non-songbirds, can offer valuable insights into the evolutionary aspects of auditory perception.

In addition, future research directions should take into account the ecological relevance of zebra finch auditory discrimination in their natural habitats. Investigating how their perceptual flexibility translates to real-world scenarios and influences social interactions can provide a holistic understanding of their song recognition abilities. This ecological perspective will bridge the gap between laboratory findings and the practical application of these perceptual abilities in the wild, offering a comprehensive view of zebra finches' auditory cognition. In conclusion, our research highlights the extraordinary perceptual flexibility of zebra finches, revealing their capacity to integrate both spectral and temporal attributes. This adaptability results from a dynamic interplay among factors such as training conditions, the nature of stimuli, and ecological relevance. The birds' adaptability for auditory perception, as a sort of multifaceted cognitive procedure influenced by various factors, does not stand alone but rather arises from the interplay among various acoustic attributes. Understanding the complex cognitive processes governing avian perceptual flexibility not only enriches our understanding of auditory perception but also provides valuable insights into cognitive abilities across diverse species.

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