

Pitch perception is not unitary: Evidence for the perception of pitch chroma in black-capped chickadees.

by

John Hoang

A thesis submitted in partial fulfillment of the requirements for the degree of

Master of Science

Department of Psychology
University of Alberta

© John Hoang, 2015

Abstract

Pitch perception is mediated by two attributes: pitch height and pitch chroma. These two attributes can be pitted against one another during an octave equivalence task in order to clarify the dominant perceptual mechanism. Pitch chroma mediates the perceptual phenomenon of octave equivalence, which occurs when two acoustic events are perceived as similar because they share the same chroma. Pitch height perception is the perception that a larger difference in frequency leads to a larger difference in perceived pitch. Previous research tested chickadees on a standardized octave equivalence task and suggested that pitch height use by chickadees may have overshadowed their ability to use pitch chroma. To disambiguate this possibility, I presented humans and chickadees with two novel discrimination tasks. Humans and chickadees were trained to discriminate three pairs of notes. After training, both humans and chickadees were presented with novel note pairs with either the same or different pitch chroma. Humans were able to transfer discrimination performance to stimuli with the same pitch chroma whereas chickadees are unable to generalize or transfer the discrimination. Results also indicate that the partial-reversal of response contingencies for pitch chroma related notes interferes with the learned discrimination. My results suggest that both humans and chickadees perceive pitch chroma; however, chickadees show preferential use of pitch height over pitch chroma.

Preface

This thesis is an original work by John Hoang. The research project, of which this thesis is a part, received research ethics approval from the University of Alberta Research Ethics Board, Project Name “Neuroethology of Songbird Acoustic Communication: Laboratory Behaviour”, AUP00000108_REN2, 5/15/2014; and “AUDITORY PERCEPTION AND COGNITION”, Pro00016997, REN3, 16/06/2013.

Some of the research conducted for this thesis forms part of a national research collaboration, led by Professor C.B. Sturdy at the University of Alberta, with Professor R. G. Weisman being the lead collaborator at Queen’s University. Professor R.G. Weisman, Professor C.B. Sturdy, and M. Hoeschele were involved in concept formation. The program referred to in chapter 2 was programmed and designed by S. Ferguson. The operant conditioning apparatus referred to in chapter 3 was designed by Professor R. G. Weisman and built by L. Omerzu. I was responsible for the data collection and analysis. R. G. Weisman and D. Cervantes assisted with the data collection.

This thesis is an original work by John Hoang. No part of this thesis has been previously published.

Acknowledgements

I would like to give my sincerest thanks to my supervisor Dr. Christopher Sturdy for all of his guidance and support throughout my degree. The many hours spent designing, interpretation, and discussing the projects comprising this thesis are greatly appreciated; without his advice this project would not have been possible. I would also like to thank my graduate committee, Dr. Pete Hurd and Dr. Marcia Spetch, for their guidance, time, and commitment as well.

I would like to also thank my lab mates, Dr. Neil McMillan, Allison Hahn, Kimberley Campbell, Jenna Congdon, Erin Scully, Diana Cervantes, and Josh Yong. In addition I would like to thank my collaborators, Dr. Marisa Hoeschele and Dr. Ronald G. Weisman. The involvement of these individuals and investment of hours in data collection and discussion have allowed this project to come to fruition.

I would like to thank the Psychology department's technicians, Lou Omerzu, Isaac Lank, Al Dennington, and Phillip May, without their support these experiments would have been accompanied by many more hours of frustration and dismay.

Finally I would like to thank my parents, Tam and Ninh Hoang, and my siblings, Janet, Jordan, and Joshua Hoang for supporting and always believing in me.

Contents

List of Tables	viii
List of Figures	ix
General Introduction	1
Evolutionary origin of Language	1
Darwin’s (Fitch’s) “Musical Protolanguage” Hypothesis	3
Models of Language Capacities: Common Decent and Convergent Evolution	5
Universal Musicality	7
Octave Equivalence and Pitch Perception	8
Chapter 2: Introduction (Experiment 1).....	10
Methods (Experiment 1)	14
Participants.....	14
Apparatus	15
Stimuli and Procedure.....	15
Results & Discussion	21
Correlations of Discrimination Success and Personal Histories.....	21
Discrimination Training and Exclusion Criteria.....	23
AP Processing Participants	24
Generalization testing	25
Failure to Generalize to Novel Note Ranges	26
Transfer Testing.....	28
Category Perception of Pitch Chroma in Transfer Testing.....	31
Conclusion	32
Tables & Figures.....	33
Figure.2.1. Transfer testing response contingencies.....	33
Figure 2.2. Learner Discrimination training	35
Figure 2.3. Non-Learner Discrimination training	36
Figure 2.4. AP possessor Discrimination training	37
Figure 2.5. Intra-octave Generalization testing.....	38
Figure 2.6. Inter-octave Generalization testing.....	39
Figure 2.7. AP possessor Inter-octave Generalization test	40
Figure 2.8. Intra-octave Original-transfer testing	41
Figure 2.9. Intra-octave Partial-reversal Transfer testing	42

Figure 2.10. Inter-octave Original-transfer testing	43
Figure 2.11. Inter-octave Partial-reversal Transfer testing	44
Chapter 3: Introduction (Experiment 2).....	45
Methods (Experiment 2)	46
Results & Discussion	54
Discrimination Training.....	54
Generalization Testing	55
Transfer Testing	57
Interference effect of the Partial-reversal of Response Contingencies	59
Transfer Discrimination training.....	60
Savings and Learning Curves	63
Alternating pattern generalization.....	64
Pitch Height Reliance over Pitch Chroma	65
Tables & Figures.....	66
Table 3.1 Group assignment Table	66
Figure 3.1. Discrimination training.....	67
Figure 3.2. Discrimination training – Vincentized Learning Curve	68
Figure 3.3. Intra-octave Generalization testing.....	69
Figure 3.4. Inter-octave Generalization testing.....	70
Figure 3.5. Intra-octave Original-transfer testing	71
Figure 3.6. Intra-octave Partial-reversal Transfer testing	72
Figure 3.7. Inter-octave Original-transfer testing	73
Figure 3.8. Inter-octave Partial-reversal Transfer testing	74
Figure 3.9. Intra-octave Original-transfer Discrimination training	75
Figure 3.10. Intra-octave Partial-reversal Discrimination training.....	76
Figure 3.11. Inter-octave Original-transfer Discrimination training	77
Figure 3.12. Inter-octave Partial-reversal Discrimination training.....	78
Figure 3.13. Transfer Discrimination training - Vincentized Learning Curves.....	79
General Discussion	80
Comparison of Pitch Use Across Species	80
Implications and Future Directions.....	83
Conclusion	85

Figure 4.1. Comparison of Discrimination training.....	86
Figure 4.2. Comparison of Intra-octave Generalization testing.....	87
Figure 4.3. Comparison of Inter-octave Generalization testing.....	88
Figure 4.4. Comparison of Intra-octave Original-transfer testing	89
Figure 4.5. Comparison of Intra-octave Partial-reversal Transfer testing	90
Figure 4.6. Comparison of Inter-octave Original-transfer testing	91
Figure 4.7. Comparison of Inter-octave Partial-reversal Transfer testing	92
References.....	93

List of Tables

Table 2.1. Transfer testing response contingencies. Table depicts the note pairs presented in each condition, and their response contingency. Black boxes indicate note pair was not presented in the condition. S+ indicates responses to the note pair was rewarded with access to food. S- indicates responses to the note pair was punished with a ‘lights out’.

Table 3.1. Group assignment Table. The table describes the division of birds into experimental groups during the Discrimination training, Generalization testing, Transfer testing, and Transfer Discrimination training phases of the experiment. For Generalization testing birds were assigned to either Intra-octave or Inter-octave condition. For Transfer testing birds were further divided into either Original-transfer or Partial-reversal condition. Group assignment was unchanged for Transfer Discrimination training.

List of Figures

Figure 2.1. Learner Discrimination training. Graph depicts the normalized average proportion of responding during Discrimination training for Learner participants. S+ stimuli range D4/D#4 and S- stimulus ranges C4/C#4 and E4/F4. Solid line indicates the average group response for participants. Dashed line indicates the expected response if participants were perfectly accurate. Error bars are \pm S.E.M.

Figure 2.2. Non-Learner Discrimination training. Graph depicts the normalized average proportion of responding during Discrimination training for Non-Learner participants. S+ stimuli range D4/D#4 and S- stimulus ranges C4/C#4 and E4/F4. Solid line indicates the average group response for participants. Dashed line indicates the expected response if participants were perfectly accurate. Error bars are \pm S.E.M.

Figure 2.3. AP possessor Discrimination training. Graph depicts the normalized average proportion of responding during Discrimination training for AP possessor participants. S+ stimuli range D4/D#4 and S- stimulus ranges C4/C#4 and E4/F4. Solid line indicates the average group response for participants. Dashed line indicates the expected response if participants were perfectly accurate. Error bars are \pm S.E.M.

Figure 2.4. Intra-octave Generalization testing. Graph depicts the normalized average proportion of responding during Generalization testing for Learner participants to six note pairs from the 4th octave. Solid line indicates the average group response for participants. Error bars are \pm S.E.M.

Figure 2.5. Inter-octave Generalization testing. Graph depicts the normalized average proportion of responding during Generalization testing for Learner participants to three note pairs from the

4th octave and three note pairs from the 5th octave. Solid line indicates the average group response for participants. Error bars are \pm S.E.M.

Figure 2.6. AP possessor Inter-octave Generalization test. Participants normalized average proportion of responding during a generalization task for AP possessor participants. Dashed line indicates expected responding based on perfect discrimination and generalization. Error bars are \pm S.E.M.

Figure 2.7. Intra-octave Original-transfer testing. Participants normalized average proportion of responding during Transfer testing for Intra-octave original-transfer participants. S+ ranges: D4/D#4 and G#4/A4. S- Ranges: C4/C#4, E4/F4, F#4/G4, and A#4/B4. Solid line indicates the average group response. Dashed line indicates expected responding based on perfect discrimination. Error bars are \pm S.E.M.

Figure 2.8. Intra-octave Partial-reversal Transfer testing. Participants normalized average proportion of responding during Transfer testing for Intra-octave Partial-reversal participants. S+ ranges: D4/D#4, F#4/G4, and A#4/B4. S- Ranges: C4/C#4, E4/F4, and G#4/A4. Dashed line indicates expected responding based on perfect discrimination. Solid line indicates the average group response. Error bars are \pm S.E.M.

Figure 2.9. Inter-octave Original-transfer testing. Participants normalized average proportion of responding during Transfer testing for Inter-octave original-transfer participants. S+ ranges: D4/D#4 and D5/D#5. S- ranges: C4/C#4, E4/F4, C5/C#5, and E5/F5. Dashed line indicates expected responding based on perfect discrimination. Solid line indicates the average group response. Error bars are \pm S.E.M.

Figure 2.10. Inter-octave Partial-reversal Transfer testing. Participants normalized average proportion of responding during Transfer testing for Inter-octave Partial-reversal Transfer participants. S+ ranges: D4/D#4, C5/C#5, and E5/F5. S- ranges: C4/C#4, E4/F4, and D5/D#5. Dashed line indicates expected responding based on perfect discrimination. Solid line indicates the average group response. Error bars are \pm S.E.M.

Figure 3.1. Discrimination training. Graph depicts the normalized average proportion of responding during Discrimination training for black-capped chickadees. S+ stimuli range D4/D#4 and S- stimulus ranges C4/C#4 and E4/F4. Solid line indicates the average group response for participants. Error bars are \pm S.E.M.

Figure 3.2. Discrimination training Vincentized learning curves. Graph depicts the normalized learning curves during Discrimination training for black-capped chickadees. Error bars are \pm S.E.M.

Figure 3.3. Intra-octave Generalization testing. Graph depicts the normalized average proportion of responding during Generalization testing for chickadees using six note pairs from the 4th octave. Solid line indicates the average group response for participants. Dashed line indicates the expected response if chickadees responded based on response contingencies. S+ stimuli range D4/D#4 and S- stimulus ranges C4/C#4 and E4/F4. Error bars are \pm S.E.M.

Figure 3.4. Inter-octave Generalization testing. Graph depicts the normalized average proportion of responding during Generalization testing for chickadees using three note pairs from the 4th octave and three note pairs from the 5th octave. Solid line indicates the average group response for participants. Dashed line indicates the expected response if chickadees responded based on response contingencies. S+ stimuli range D4/D#4 and S- stimulus ranges C4/C#4 and E4/F4. Error bars are \pm S.E.M.

Figure 3.5. Intra-octave Original-transfer testing. Participants normalized average proportion of responding during Transfer testing for Intra-octave Original-transfer condition chickadees using six note pairs from the 4th octave. S+ ranges: D4/D#4 and G#4/A4. S- Ranges: C4/C#4, E4/F4, F#4/G4, and A#4/B4. Solid line indicates the average group response. Dashed line indicates expected responding based on perfect discrimination. Error bars are \pm S.E.M.

Figure 3.6. Intra-octave Partial-reversal Transfer testing. Participants normalized average proportion of responding during Transfer testing for Intra-octave Partial-reversal condition chickadees using six note pairs from the 4th octave. S+ ranges: D4/D#4, F#4/G4, and A#4/B4. S- Ranges: C4/C#4, E4/F4, and G#4/A4. Dashed line indicates expected responding based on perfect discrimination. Solid line indicates the average group response. Error bars are \pm S.E.M.

Figure 3.7. Inter-octave Original-transfer testing. Participants normalized average proportion of responding during Transfer testing for Inter-octave Original-transfer condition chickadees using three note pairs from the 4th octave and three note pairs from the 5th octave. S+ ranges: D4/D#4 and D5/D#5. S- ranges: C4/C#4, E4/F4, C5/C#5, and E5/F5. Dashed line indicates expected responding based on perfect discrimination. Solid line indicates the average group response. Error bars are \pm S.E.M.

Figure 3.8. Inter-octave Partial-reversal Transfer testing. Participants normalized average proportion of responding during Transfer testing for Inter-octave Partial-reversal Transfer condition chickadees using three note pairs from the 4th octave and three note pairs from the 5th octave. S+ ranges: D4/D#4, C5/C#5, and E5/F5. S- ranges: C4/C#4, E4/F4, and D5/D#5. Dashed line indicates expected responding based on perfect discrimination. Solid line indicates the average group response. Error bars are \pm S.E.M.

Figure 3.9. Intra-octave Original-transfer Discrimination training. Participants normalized average proportion of responding during Transfer Discrimination training for Intra-octave original-transfer condition chickadees using three note pairs from the 4th octave. S+ ranges: G#4/A4. S- Ranges: F#4/G4, and A#4/B4. Solid line indicates the average group response. Dashed line indicates expected responding based on perfect discrimination. Error bars are \pm S.E.M.

Figure 3.10. Intra-octave Partial-reversal Transfer Discrimination training. Participants normalized average proportion of responding during Transfer Discrimination training for Intra-octave original-transfer chickadees using three note pairs from the 4th octave. S+ Ranges: F#4/G4, and A#4/B4. S- ranges: G#4/A4. Solid line indicates the average group response. Dashed line indicates expected responding based on perfect discrimination. Error bars are \pm S.E.M.

Figure 3.11. Inter-octave Original-transfer Discrimination training. Participants normalized average proportion of responding during Transfer Discrimination training for Inter-octave original-transfer chickadees using three note pairs from the 5th octave. S+ ranges: D5/D#5. S- ranges: C5/C#5, and E5/F5. Dashed line indicates expected responding based on perfect discrimination. Solid line indicates the average group response. Error bars are \pm S.E.M.

Figure 3.12. Inter-octave Partial-reversal Transfer Discrimination training. Participants normalized average proportion of responding during Transfer Discrimination training for Inter-octave Partial-reversal Transfer chickadees using three note pairs from the 5th octave. S+ ranges: D4/D#4, C5/C#5, and E5/F5. S- ranges: C4/C#4, E4/F4, and D5/D#5. Dashed line indicates expected responding based on perfect discrimination. Solid line indicates the average group response. Error bars are \pm S.E.M.

Figure 3.13. Discrimination training Vincentized learning curves. Graph depicts the normalized learning curves during Transfer Discrimination training for black-capped chickadees. Error bars are \pm S.E.M.

Figure 4.1. Comparison of Discrimination training. Figure depicts the responses for humans and chickadees in a go/no-go discrimination task using three note pairs from the 4th octave. The solid line represents the human responses. The dashed line represents the chickadee response. Error bars are \pm S.E.M.

Figure 4.2. Comparison of Intra-octave Generalization testing. Figure depicts the responses for humans and chickadees in a generalization task using six note pairs from the 4th octave. The solid line represents the human responses. The dashed line represents the chickadee response. Error bars are \pm S.E.M.

Figure 4.3. Comparison of Inter-octave Generalization testing. Figure depicts the responses for humans and chickadees in a generalization task using three note pairs from the 4th octave and three note pairs from the 5th octave. The solid line represents the human responses. The dashed line represents the chickadee response. Error bars are \pm S.E.M.

Figure 4.4. Comparison of Intra-octave Original-transfer testing. Figure depicts the responses for humans and chickadees in the Transfer testing task using six note pairs from the 4th octave. The solid line represents the human responses. The dashed line represents the chickadee response. Error bars are \pm S.E.M.

Figure 4.5. Comparison of Intra-octave Partial-reversal transfer testing. Figure depicts the responses for humans and chickadees in the Transfer testing task using six note pairs from the 4th octave. The solid line represents the human responses. The dashed line represents the chickadee response. Error bars are \pm S.E.M.

Figure 4.6. Comparison of Inter-octave Original-transfer testing. The figure depicts the responses for humans and chickadees in the Transfer testing task using three note pairs from the 4th octave and three note pairs from the 5th octave. The solid line represents the human responses. The dashed line represents the chickadee response. Error bars are \pm S.E.M.

Figure 4.7. Comparison of Inter-octave Partial-reversal Transfer testing. The figure depicts the responses for humans and chickadees in the Transfer testing task using three note pairs from the 4th octave and three note pairs from the 5th octave. The solid line represents the human responses. The dashed line represents the chickadee response. Error bars are \pm S.E.M.

General Introduction

Evolutionary origin of Language

A feature of human cognition is the ability to communicate complex concepts using a set of mutually understood vocalizations in a hierarchically structured manner, commonly referred to as language (Chomsky, 1956). Language facilitates the communication of extremely complex ideas between two or more individuals with precision and clarity. For example, the sentence *Sandra, can you please purchase strawberries when you go to the store this afternoon?* identifies the individual the speaker is addressing, the action, the subject, the time the action is to occur, and the location of the request. The use of language is one capacity that distinguishes humans from other animal species, even our closest primate relatives. The apparent uniqueness of the human language capacity is a mixed blessing, as it limits the traditional scientific methods in studying the evolutionary development and origin of language.

It is important to first define what is meant by language, and why it is considered a uniquely human ability. Although there exist varying definitions of language in the scientific literature, there are a few characteristic features common to many definitions. One feature is that a language must contain a hierarchical syntactic or grammatical structure that is agreed upon by individuals that communicate in that particular language (for reviews, see: Bolhuis, Tattersall, Chomsky, & Berwick, 2014; Hauser, & McDermott, 2003). Chomsky (1986) originally drew attention to the fact that, independent of education, nearly all speakers of a language are able to identify grammatical and ungrammatical sentence structures. Chomsky used the phrase “knowledge of language” to refer to this underlying rule set that defined grammatical and ungrammatical sentence structure in every language. A second feature is that individual elements

in a language have symbolic lexical meanings; that is, a word used in place of the object must be able to invoke the same reaction the object would. The symbolic meaning of a language element must be learned and agreed upon by all speakers of the language. The capacity for language to elicit mental abstractions is key to its function and efficiency. If an individual was required to physically indicate the object of a request, this would severely limit the value of the communication system. The symbolic or referential value of language is demonstrated by the use of language in writing. For example, verbs do not resemble the action performed, but the phrase, “Billy ran quickly,” nonetheless will illicit the mental imagery of an individual in a state of rapid locomotion caused by the movement of Billy’s legs. The third, and arguably the most useful, feature is language generativity. Language generativity is the concept that an individual, from a rehearsed repertoire, can produce novel sentences and understand sentences never before heard; thus allowing the communication of novel concepts and ideas between individuals. Given these criteria as the definition of language, humans are the only extant animal species known to have the mental faculty of language.

The uniqueness of the human capacity for language enables humans to communicate complex cognitive concepts with efficiency and accuracy, but the uniqueness of this capacity impedes the search for the evolutionary origin of language. The traditionally-preferred methodology to study evolutionary traits relies on one characteristic feature of evolution: divergent evolution. Divergent evolution, the concept that species share a common ancestor, results from the differentiation of species through successive changes over the course of millions of years. Traditional methodologies use each divergent species as a data point to understand the evolutionary origin of species specific traits through the examination of fossil records. Problematically, language is a mental faculty and leaves no fossil records, limiting the biological

perspective in its approach to determining the evolutionary origin of language. Additionally, the human vocal structure (the pharyngeal region, Lieberman, Klatt, & Wilson, 1969; and position of the hyoid bone, Corballis, 1992), allows for the production of highly variable vocalizations not reproducible in other mammalian species. The capacity for language and human vocal complexity distinguishes our species from all other extant species, and poses a significant issue for the traditional methods of the biological approach which rely on analysis of divergent evolution.

Darwin's (Fitch's) "Musical Protolanguage" Hypothesis

Among the main theories that have been proposed for the origin of language is Darwin's "Musical Protolanguage" hypothesis (Darwin, 1871; Fitch, 2006). The hypothesis was originally proposed by Darwin in "The Decent of Man and Selection in Relation to Sex"; more recently, Fitch has modernized and championed the hypothesis. Darwin's (1871) original proposition suggested that the language faculty developed in stages: first the cognitive capacity for language must develop, followed by an intermediary communication system, and finally the faculty for language. The Musical Protolanguage hypothesis suggests that the intermediary communication system was based on an "emotionally-expressive musical proto-language" (Fitch, 2009, pg. 3), which shared little resemblance to modern music systems, but was a primitive precursor to both the music and language faculties. The transition from the proto-language to true meaningful language would have developed as the hominid lineage developed more sophisticated vocal abilities and attributed specific meanings to vocalizations. The initial acquisition of meaningful vocalizations would then promote the development of complex vocal structures and language

capacities. Fitch (2009) argues that musical protolanguage would have existed in a form that fulfilled key social functions such as courtship, territory defence, and competitive displays. Darwin documented the similarities between human and songbird vocal learning and how songbird vocalizations could be analogous to the proposed musical protolanguage (as cited by Fitch, 2009). Evidence for learned communication has been found in at least six clades of vocal learning animals: cetaceans, pinnipeds, bats, parrots, hummingbirds, and oscine songbirds (Janik, & Slater, 1997; Jarvis, 2004). These documented instances of convergent evolution may serve as the alternative models to the primate lineages in the study of language capacities.

Darwin's Musical Protolanguage hypothesis also has difficulties when applied to songbird vocalizations. Fitch (2005) suggested that two major differences existed between human and songbird vocal learning: (1) human males and females produce song and vocalizations in a similar manner; and (2) human infants' language capacities are expressed in early ontogeny. In recent years, empirical evidence has weakened these discrepancies in vocal learning between humans and songbirds. The traditional view point of the scientific community is that female songbirds do not produce song (Garamszegi, Pavlova, Eens, & Møller, 2007); in this context song refers to the production of vocalizations intended for the deterrence of intra-sexual competitors, maintain intra-pair contact, individual identification, mate attraction (for a review: Nottebohm, 1972), solicitation of copulation (Brockway, 1969), and territory defence (Weeden & Falls, 1959; Searcy, Anderson, & Nowicki, 2006). Evidence counter to this view has been provided by Garamszegi, et al. (2007) where comprehensive analysis of European songbird species found that females produced song in 101 of 233 examined species; in 124 of the 233 species there was no information on female song production and more importantly in only 8 species were females confirmed to not produce song. The most significant finding to the current

discourse was that through analysis of cladistics modeling, Garamszegi and colleagues identified 3 songbird families in which female song production could be the ancestral state. Garamszegi, et al. (2007) further suggest that in the common ancestor to all songbirds' males and females may have shared a more egalitarian role in song production; a role lost through sexual selection in some species. Human language capacities develop remarkably early in ontogeny; fetuses have been shown to develop language preferences to their mother's voice *in utero* and are expressed as infants (DeCasper & Fifer, 1980; Spence & Freeman, 1996). Although evidence is limited in songbirds, similar findings have been found in the Australian superb fairy-wren. *In ovo* fairy-wrens learn a vocal password from the attending female during incubation, and after hatching use the learned vocal element as their begging call (Colombelli-Négrel, Hauber, & Kleindorfer, 2014). Together, this growing evidence is congruent with the notion that language capacities in songbirds may have developed from an ancestral state analogous to the hominid lineage.

Models of Language Capacities: Common Decent and Convergent Evolution

The unique nature of the human language faculty and vocal capacities present obstacles in the study of the evolution of language. As previously mentioned, a hallmark characteristic of the human language faculty is vocal learning. Despite significant effort, researchers have been unable to demonstrate language faculties in our closest primate relatives (for a review, see Fitch, 2005), and with the exception of a few notable case studies (e.g., Koko the low-land gorilla and Kanzi the chimpanzee) demonstrated language capacities in non-human primates has been limited (for a review, see Egnor & Hauser (2004); Lemasson, Ouattara, Petit, & Zuberbühler, 2011). Non-human primate vocalizations are by and large produced in a stereotypical manner

and have been shown to be resistant to developmental interference (for a review, see Janik & Slater, 1997); there is mixed evidence for vocal learning in non-human primates. Strong evidence against vocal learning has been demonstrated in squirrel monkeys (*Saimiri sciureus*); squirrel monkeys were found to produce acoustically-normal vocalizations after acoustic isolation (Winter, Handley, Ploog, & Schoot, 1973) and deafening procedures (Talmage-Riggs, Winter, Ploog, & Mayer, 1972) during development. Regional variations in vocal production have been observed in: saddle-backed tamarins, *Saguinus fuscicollis* (Hodun, Snowdon, & Soini, 1981); Japanese macaques, *Macaca fuscata* (Masataka & Fujita, 1989); chimpanzees, *Pan troglodytes verus* (Crockford, Herbingre, Vigilant, & Boesch, 2004); and gibbons, *Hylobatidae* spp. (Mitani, 1987). A major complication in these studies is the inability to exclude genetic factors as a source of regional variations in vocal production. Stronger evidence for vocal learning comes from reports of vocal convergence in unrelated adult individuals. Pygmy marmosets, *Cebuella pygmaea* (Snowdon & Elowson, 1999) and chimpanzees (Mitani & Gros-Louis, 1998) have been observed to converge in vocal production with pair mates. Taken together, current evidence suggests that non-human primate vocal learning is limited and is constrained by genetically pre-determined vocal plasticity within each species.

Paradoxically, of all non-human animal groups, songbirds are documented as the most successful vocal learners (Egnor & Hauser, 2004). Songbirds, although taxonomically distant to humans, demonstrate several key language capacities that warrant discussion on their use as model species: vocal learning (zebra finches, *Taeniopygia guttata*: Vicario, Naqvi, & Raksin, 2001; swamp sparrows, *Melospiza georgiana*: Marler & Peters, 1982; black-capped chickadees, *Parus atricapillus*: Hughes, Nowicki, & Lohr, 1998; budgerigars, *Melopsittacus undulatus*: Farabaugh, Linzenbold, & Dooling, 1994), group convergence of vocal production (black-

capped chickadees: Nowicki, 1989; white-crowned sparrows, *Zonotrichia leucophrys*: Marler & Tamura 1964), and most significantly, song production functions similarly to Darwin's proposed Musical Protolanguage. Songbirds, when compared to non-human primates, provide several important advantages as an alternative model species: developmental experience can be well controlled (Shackleton & Ratcliff, 1993; Hahn et al., 2015), the effects of developmental experience on vocal learning are well documented, and the avian song system contains many analogous neural structures providing a simplified neural auditory system for comparative study (Doupe & Kuhl, 1999). Given the similarities, bird song has value in the study of language as an analogous vocal system to human language.

Universal Musicality

The proposition that the human language faculty developed from a “musical protolanguage”, posits that there is a biological basis to the perception of musicality. I would therefore expect to find near-universal perception of musicality across human cultures, perception of musicality early in ontology, and perception of musicality to be conserved in non-human primates and protolanguage candidate groups. There is evidence to support the near-universal perception of pitch contour, musical intervals, rhythm (for review, see: Trehub, 2000), melody (for review, see: Stevens, 2004), prosody (Fernald et al., 1989), and consonance-dissonance (American-Japanese: Butler & Daston, 1968; Western-Raga-rasa: Balkwill & Thompson, 1999). Octaves have also been proposed as a musical universal; however, experimental demonstration of octave perception has been problematic (e.g., Kallman, 1982). To further support the biological origin of musicality, pre-linguistic infants have been reported to

perceive of pitch contour (Nazzi, Floccia, Bertoncini, 1998), melody (Plantinga & Trainor, 2005), prosody (Fernald et al., 1989), consonance-dissonance (Zentner & Kagan, 1998), and octaves (Demany & Armand, 1984). Though limited, there is evidence for the perception of musicality in non-human primates: Japanese macaques are able to discriminate consonance and dissonant chords (Izumi, 2000), and rhesus macaques (*Macaca mulatta*) are reported to perceive octaves (Wright, Rivera, Hulse, Shyan, & Nejdworth, 2000) and rhythm (Honing, Merchant, Haden, Prado, & Bartolo, 2012). In songbirds, there is evidence for perception of consonance-dissonance (Java sparrows, *Padda oryzivora*, Watanabe, Uozumi, & Tanaka, 2005; and European starlings, *Sturnus vulgaris*, Hulse, Bernard, & Braaten, 1995), pitch perception (black-capped chickadees, Njegovan & Weisman, 1997; starlings, cowbirds, *Molothrus ater*, and mockingbirds, *Mimus polyglottos*, Hulse & Cynx, 1985), and pitch contour (European starlings, Hulse & Cynx, 1986). The cross-cultural perception of musicality directs the examination of fundamental perceptual abilities in other animal groups. There is growing evidence to support the perception of these musical fundamentals in non-human primates and protolanguage candidate groups, such as songbirds.

Octave Equivalence and Pitch Perception

An octave describes a musical relationship closely tied to a physical property of acoustic sound waves. Two acoustic events are separated by an octave when the second event is half or twice the frequency of the first (i.e., a halving or doubling) (Shepard, 1982). Octave equivalence describes when two acoustic events separated by an octave are perceived as being more similar than two events separated by a frequency change that is less than an octave (Shepard, 1982).

Two properties of pitch are responsible for the perception of pitch: pitch height and pitch chroma. Pitch chroma is responsible for the perception of octave equivalence, and describes a non-linear relationship to frequency where increases in frequency do not necessarily lead to larger differences in pitch chroma. Pitch height describes a log-linear relationship to frequency where larger differences in frequency are perceived as larger differences in pitch height. Pitch height and pitch chroma are in conflict during an octave equivalence task, and the selective use of pitch chroma over pitch height would result in demonstration of octave equivalence.

Absolute pitch (AP) is the ability to identify or recreate a given musical note without use of a reference tone; while relative pitch (RP) is the ability to do so with the use of a reference tone. In humans the ability of AP perception is found in approximately 1 of 1000 individuals. Interestingly, individuals identified as AP possessors also have an exceptional ability to also identify musical notes based on pitch chroma (Miyazaki, 1988). RP perception evidence to suggest RP perception is learned at an early age and that there is a perceptual shift from absolute pitch perception to relative pitch perception in young children from ages 3-6 (Sergeant, & Roche, 1973). Chickadees are able to perceive both AP and RP, but have a preference to for using AP over RP (MacDougall-Shackleton and Hulse, 1996).

Previous research examining octave equivalence in humans and black-capped chickadees has suggested that chickadees are able to generalize a discrimination task to a novel octave range but may have relied on pitch height (Hoeschele, Weisman, Guillette, Hahn, & Sturdy, 2013). Due to possible alternative interpretations it is unclear if chickadees are unable to use pitch chroma or if they do not rely on pitch chroma perception. This study builds on the previous work and aims to clarify if black-capped chickadee songbird is able to perceive pitch chroma.

Chapter 2: Introduction (Experiment 1)

The first experiment examined octave equivalence in human participants using a Go/No-Go discrimination task modified from Hoeschele et al. (2013). This functioned as a positive control for my comparative methodology as humans are known to perceive octaves. The second experiment examined octave equivalence in black-capped chickadees using the verified methodology. The primary modification to the experimental design from Hoeschele et al. (2013), was the range of frequencies used in discrimination training, generalization testing, and transfer testing. Hoeschele et al. (2013) trained human participants and chickadees to discriminate note ranges with all 12 notes of the 4th octave and examined generalization and transfer to the 5th octave. In the current experiment I trained human participants and chickadees with 6 notes (C4-F4) and examined generalization to either the remaining six note of the 4th octave (F#4-B4) or 6 notes from the 5th octave (C5-F5). This modification differentiates generalization strategies based on pitch height and pitch chroma. I tested for octave equivalence by assessing for generalization; this was then followed by a partial-reversal design to test for category perception based on pitch height and pitch chroma. Previous research suggested that chickadees solved an octave discrimination task by using an alternating frequency range strategy (AFRS) (i.e., S+ is followed by S- and is followed by S+) that relied on pitch height (Hoeschele et al., 2013). The results did not conclusively suggest that chickadees could not perceive pitch chroma, but that pitch chroma was not relied on during the octave equivalence discrimination task.

Attempts at the experimental detection of octave equivalence in human participants have yielded mixed results despite strong anecdotal evidence of octave equivalence use in humans (e.g., choir members will sing in different octaves [Soprano: C4-C6, Alto: G3-G5, Tenor: C3-C5, Baritone: G2-G4] but can all match the same key while singing). Allen (1967) found that octave equivalence perception depended heavily on musical experience, where non-musicians did not demonstrate any perception of octave equivalence. Counter to this, Kallman (1982) found that both musicians and non-musicians perceived octaves, but the frequency range of the stimuli had a significant effect on the perception of octave equivalence. To mitigate the variability in octave equivalence detection, I used the methodology of Hoeschele, Weisman, and Sturdy (2012) which was used to detect octave equivalence in humans.

The purpose of Experiment 1 was to test a variation of a procedure used in Hoeschele et al. (2012), which would then be adapted for a comparative experiment in chickadees. My study relied on two methods to demonstrate the perception of octave equivalence: generalization of learned response contingencies and the partial reversal of pitch chroma and pitch height categories. This design is predicated on the perceptual similarity between notes that share pitch chroma; that is, a C4 note sounds similar to a C5 note and forms a natural stimulus-class. Here I attempted to establish the perception of octave equivalence by testing for the category perception of pitch chroma (e.g., all C notes sound similar and will be grouped as similar).

In a demonstration of generalization, Hearst, Koresko, and Poppen (1964) trained pigeons to respond to orientations of line-tilts, and tested the pigeons using a continuum of varying line-tilts. Results suggested that perceptually similar stimuli can exert stimulus control, on response

patterns, without explicit training with the novel stimuli, and thus can be used as a measure of perceptual similarity.

Partial reversal designs can be used to demonstrate stimulus equivalence, a feature of category discriminations. Partial reversals function on the assumption that a given set of stimuli are perceived as a single category, e.g., an apple, pear, and banana are all fruits. Based on this idea studies have used many-to-one discrimination procedures to produce stimulus-class formations of artificial categories in pigeons (hues and line orientation: Zentall, Steirn, Sherburne, & Urcuioli, 1991; and pictures: Vaughan, 1988) and rats (colors and line orientation: Nakagawa, 1986). Although hues and lines are perceptually different, due to training subjects begin to treat these stimuli as being similar; this process is referred to as stimulus-class formation and can be considered an artificial stimulus-class. Once the subject has been trained to discriminate two artificial stimulus-classes (one S+ and one S- class), response contingencies were manipulated in one of two conditions: a partial-reversal or a full-reversal. In the partial-reversal condition half the stimuli in each stimulus-class, both the S+ and S-, was reinforced and the other half was non-reinforced. The full-reversal group had the response contingencies reversed so that the reinforced stimulus-class (S+) became non-reinforced (S-) and vice versa. If the subjects formed stimulus-classes during training then the full-reversal group would relearn the new response contingencies faster. Alternatively, if subjects did not form stimulus-classes then the partial-reversal group would learn the new response contingencies faster, because the subjects would only need to relearn stimulus-response contingencies for half the stimuli.

The current experiment tested two hypothesis: one based on Hoeschele et al. (2013) which suggested chickadees learned to use an AFRS; and that chickadees do perceive pitch

chroma but failed to demonstrate this ability. To test if chickadees had learned to use an AFRS, tested for generalization to the extended pattern, e.g., S-/S+/S- would be continued as S-/S+/S-/S+/S-/S+, by introducing and additional six notes from the 4th octave (F#4-B4). Two patterns were tested an interruption of the AFRS, *Intra-octave Original-transfer* [Fig 2.1.2A], and a continuation of the AFRS *Intra-octave Partial-reversal* [Fig 2.1.2B]. The experiment used a partial-reversal design, where half of all stimuli to be presented during the partial-reversal are explicitly trained to test for pitch chroma perception. Other experiments have trained all stimuli as to form artificial stimulus-classes, but I am attempting to detect octave equivalence, where stimuli that share pitch chroma are perceived as categorically similar and therefore should not require explicit training. I predicted that using a partial-reversal based on pitch chroma, *Inter-octave Partial-reversal* [Fig 2.1.2C], would lead to decreased performance due to the perceptual similarity of the musical notes, while mirrored reinforcement contingencies, *Inter-octave Original-Transfer* [Fig 2.1.2D], would lead to improved performance.

Methods (Experiment 1)

Participants

Two hundred and fourteen undergraduate students at the University of Alberta and 28 undergraduate students from Queen's University enrolled in a first-year psychology course participated in the experiment for course credit. Participants provided personal information (age, gender) and their musical training and language histories (first language, years spoken, years of training, and countries of residence). Each participant gave informed written consent. Experimental protocols were approved by the General Research Board at Queen's University and Research Ethics Board at the University of Alberta.

The participants ranged in ages from 17 to 36 years of age, $M = 19$; 56 participants identified as male and 157 identified as female. Eight participants were excluded from data analysis due to not completing the experiment. Three participants were identified as AP possessors using a pitch identification task previously used by Hoeschele et al. (2012), and were analysed separately from non-AP possessors.

From the musical history surveys, 125 participants had musical training with at least one musical instrument; of these, sixty-seven participants had experience with at least two instruments. Seventy-seven participants listed piano experience in their musical history. The number of years of training ranged from one year to thirty-six years (cumulative over multiple instruments), $M = 7.1$. Eighty-eight participants did not have formal musical training.

From the language history surveys, 129 participants identified English as their native language, 13 participants identified Mandarin as their native language, eight participants

identified Cantonese as their native language, one participant identified Vietnamese as their native language, and 63 participants identified various other languages as their native language.

Apparatus

During the experiment, each participant was seated in front of either an Asus P6T SE desktop or a Toshiba 149 Tecra laptop computer. Each computer was equipped with a set of Sennheiser HD 580 pro 64 headphones (Wedemark, Lower Saxony, Germany), a custom experimental program, and a Creative Sound Blaster (Singapore, Singapore) Audigy SE soundcard (CA-0106 audio processor, with a 100dB signal-to-noise ratio and frequency response < 10 Hz – 40 kHz).

Stimuli and Procedure

Participants were randomly assigned to testing conditions. Randomization was balanced for gender, number of participants that met performance criteria, and musical experience to maintain an approximately equal number of participants in each group. The octave equivalence task consisted of three phases: discrimination training, generalization testing, and transfer testing. Participants were randomly assigned to *Interoctave* and *Intraoctave* experimental conditions for Generalization testing and further assigned to *Original-transfer* and *Partial-reversal* discrimination condition during the Transfer testing stage.

Participants initiated a trial by using the mouse and an on-screen cursor to select the “Play Note” button and were presented with a tone when the participant clicked the “Play Note” button. A trial began only after participant had clicked the “Play Note” button. If participants selected the “S+” button after hearing a ‘*go*’ tone the word “correct” would appear in a box adjacent to the S+ button. If the participant selected the “S+” button after hearing a ‘*no-go*’ tone the word “incorrect” would appear in the box adjacent to the S+ button. If no response was made after a go or no-go trial, the trial ended after 3s without feedback.

Stimuli. Sine-wave stimuli were generated using Signal 5.15.02 (Engineering Design, Berkeley, CA). Sine-wave tones were generated at frequencies of successive chromatic musical notes from C4 to F5. To provide controls for pitch height and amplitude confounds, each frequency was synthesised to play at 70dB in half the trials and 80dB in the other half. Tones were 500ms in duration, constructed at 16-bit, 44.1 kHz sampling rate, and ramped upwards at onset and downwards at offset for 5 ms, respectively.

Discrimination training. Participants were asked to classify notes into two categories (go and no-go) in an auditory discrimination task. No instructions were provided regarding the composition of each category. Participants were informed that the task was a test of their perceptual categorization ability, but were not informed the test was for octave equivalence.

Participants were presented with six note frequencies during training: C4, C4#, D4, D4#, E4, F4. Each note was presented at 70dB and 80dB. Participants were given a short practice

session with six tones to acquaint participants with the testing apparatus, and to adjust headset volume to a comfortable level. The six training notes were divided into three pairs: C4/C4#, D4/D4#, E4/F4. Go responses to notes D4 and D4# were reinforced with positive feedback, while responses C4, C4#, E4, and F4 tones were punished with negative feedback. If the “S+” button was selected to D4 or D4# then the word “correct” appeared adjacent to the “S+” button, while the “S+” button was selected to C4, C4#, E4, or F4 then the word “incorrect” appeared. Each participant completed a total of 180 trials in this stage of the experiment.

Participants initiated a trial by selecting the “Play Note” button and heard tone randomly selected from the twelve notes without replacement. Once a stimulus was presented participants were allowed two seconds to respond by selecting a “S+” button to indicate the tone belonged to the arbitrary group, this was a ‘go’ response. If a ‘go’ response was made to D4 or D4# then the word “correct” appeared adjacent to the “S+” button, while if a ‘go’ response was made to C4, C4#, E4, or F4 then the word “incorrect” appeared and participants would not be able to start the next trial for three seconds. If participants did not make a selection after three seconds, the trial timed out and participants were allowed to request the next trial; this was a ‘no-go’ response.

Generalization testing. Participants were presented with twelve notes total, six novel notes in addition to notes from *Discrimination training*. Participants were assigned to one of two conditions: Intra-octave or Inter-octave. The Intra-octave condition was presented with tones C4, C4#, D4, D4#, E4, F4, F4#, G4, G4#, A4, A4#, and B4; while the Inter-octave condition was presented with tones C4, C4#, D4, D4#, E4, F4, C5, C5#, D5, D5#, E5, and F5. Each note was presented three times each at 70dB and 80dB. Each participant experienced a total of 72 trials in

this stage of the experiment. I conducted the generalization phase of the experiment in the absence of reinforcement (positive feedback) or punishment.

Transfer testing. Participants in each testing condition (Inter-octave and Intra-octave) were further assigned to Original-transfer or Partial-reversal condition. The response contingencies for transfer stimuli differed for the Original-transfer and Partial-reversal conditions. Response contingencies remained the same for the six notes used in Discrimination training (C4, C4#, D4, D4#, E4, F4) [Fig 2.1.1]; response contingencies were manipulated for the Inter-octave and Intra-octave notes. Each participant, in all conditions, experienced a total of 240 trials in this stage of the experiment.

The Intra-octave condition was presented with frequencies for C4, C4#, D4, D4#, E4, F4, F4#, G4, G4#, A4, A4#, and B4. For the Intra-octave Original-transfer condition, responses to D4/D4# and G4#/A4 were reinforced, while responses to C4, C4#, E4, F4, F4#, G4, A4#, and B4 were not reinforced [Fig 2.1.2A]. For the Intra-octave Partial-reversal condition, responses to D4/D4#, F4#/G4, and A4#/B4 were reinforced, while responses to C4, C4#, E4, F4, G4#, and A4 were not reinforced [Fig 2.1.2B].

The Inter-octave condition was presented with frequencies for C4, C4#, D4, D4#, E4, F4, C5, C5#, D5, D5#, E5, and F5. For the Inter-octave Original-transfer condition, responses to D4/D4# and D5/D5# were reinforced, while responses to C4, C4#, E4, F4, C5, C5#, E5, and F5 were not reinforced [Fig 2.1.2C]. For the Inter-octave Partial-reversal condition, responses to

D4/D4#, C5/C5#, and E5/F5 were reinforced, while ‘go’ responses to C4, C4#, E4, F4, D4, and D4# were not reinforced [Fig 2.1.2D].

Absolute Pitch Testing. Using a procedure developed in Hoeschele et al. (2012) and adapted from Athos et al. (2007), sine wave tones were presented in a test in which each note was played for 1,000 ms. Note durations and frequencies for our AP test were adapted from the procedure used by Athos et al. (2007). The notes presented were D#2, F2, F#2, G#2, A#2, B2, C#3, D#3, E3, F3, G3, G#3, C4, C#4, D4, D#4, F4, F#4, A4, C5, C#5, D5, E5, F#5, G5, G#5, A5, A#5, C6, D6, A6, B6, C#7, D#7, F#7, B7, E8, F#8, G8, A#8. The test began after a short eight trial practice session. During the practice session and the test, the participant clicked on the “Play” button at the top of the screen and heard a tone selected randomly without replacement from the 40 test tones. To “name” the musical note corresponding to a tone, the participant clicked on one of 12 black and white piano keys shown on the screen. The test continued without feedback until the participant heard all 40 tones.

In the note-naming tests, I identified AP possessors using the same scoring protocol used by Athos et al. (2007): 1 point for each correct identification, and 0.75 points for responses to notes ± 1 semitone from the correct note. Individuals who scored twenty points or above were classified as AP possessors.

Learner vs Non-Learner Designation. Participants were screened into two groups, *Learners* and *Non-Learners*. This experiment was designed to test the generalization of learned

reinforcement contingencies, and the confounding variable of Non-Learners was controlled for by removing data of participants identified as Non-Learners. Learners were defined as participants who responded to the reinforced stimulus range more often overall than to both non-reinforced stimulus ranges during the training phase. This distinction was used to exclude Non-learner participants from further data analysis.

AP possessors. Data from individuals identified as AP possessors were removed from statistical analysis due to their exceptional discrimination abilities. Three individuals were identified as AP possessors, two possessors were in the *Inter-octave* condition and one in the *Intra-octave* condition.

Response Measures. To minimize individual variation in go bias, I report the individually normalized and averaged percent of response across each note or note range. Normalization was accomplished by determining a participant's highest response rate to all notes, and using this number to normalize (e.g., responses to C4 = 0.8, C4# = 0.6, and D4 = 0.2; normalization would result in values of C4 = 1.0, C4# = 0.75, and D4 = 0.25).

Statistical Analysis. All statistical analyses were carried out using the IBM SPSS v20 statistical package. For statistical analysis the S+ and S- note pairs were averaged for each S+

and S- range. All repeated measures ANOVAs were accompanied by a Mauchly's Test of Sphericity. If the assumption of sphericity was violated at $p = 0.02$, then adjustments were made to the degrees of freedom using Greenhouse-Geisser to determine the critical F-value.

Results & Discussion

Correlations of Discrimination Success and Personal Histories

Due to testing of multiple correlations, family-wise error was corrected for using a Bonferroni correction ($\alpha = 0.0125$, for the 4 correlational analyses that follow).

Gender. Using a Pearson's bivariate correlation, I found that there was no statistically significant correlation between gender of the participant and success in learning the discrimination task ($r_{pb} = -0.070$; $p = 0.311$).

Years of musical training. Using a Pearson's correlation, I found that there was no statistically significant correlation between years of musical training and success in learning the discrimination task ($r = 0.029$; $p = 0.67$).

Musical instrument. Using a Pearson's bivariate correlation, I found that there was a statistically significant correlation between musical training with the piano and success in learning the discrimination task ($r_{pb} = 0.213$; $p = 0.002$). No other instrument types were found to have a statistically significant correlation with success in the discrimination task

Tonal language experience. Using a Pearson's bivariate correlation, I found that there was no statistically significant correlation between experience with the tonal native language, Cantonese, of the participant and success in learning the discrimination task ($r_{pb} = -0.028$; $p = 0.680$). No other languages were found to have a statistically significant correlation with success in the discrimination task.

Surprisingly, I found that years of musical experience did not share a significant relationship with discrimination success. Instead I found that participants who had trained with pianos performed better on the discrimination task. This relationship is particularly interesting as studies have reported pianists have the widest frequency range thresholds for musical pitch discriminations (Kishon-Rabin, Amir, Vexler, & Zaltz, 2001), suggesting pianists would have poorer pitch discrimination compared to other musicians. It is possible that the innate properties of the piano match the frequencies selected to represent musical notes in my study. When tasked with adjusting tones to their matching octave, individuals induce a stretch in the size of the octave; this octave stretch amounts to 0.15 of a semitone or equivalent to a ratio of 2.009:1 and increases in higher registers (Dowling & Hardwood, 1986). Instruments are tuned to this stretched ratio, but pianos are tuned with a stretch that is approximately half of that found for the subjective tuning of pitches. Piano pitches are therefore more similar to frequencies used in this

experiment, and may have resulted in a more familiar octave ratio for pianists. Alternatively, the inherent qualities of the instrument could have played a role; that is, piano keys are tuned during production so the A4 key should be 440 Hz but a violin must be skillfully played by the musician to produce the same frequency. As such, the frequencies recognized as an A4 may vary between individuals. A possible alternative explanation is that the individuals identified as musicians are not all currently active musicians and by including non-active musicians mitigates any advantage in pitch acuity active musicians have in our task.

Discrimination Training and Exclusion Criteria

My results indicate that individuals identified as Learner participants did, in fact, learn the discrimination of the S+ and S- ranges. One hundred and fifty-three participants were identified as having learned the discrimination based on response criteria during discrimination training (a higher proportion of responding to S+ stimuli than S- stimuli). Statistical analyses were carried out using pairwise planned comparisons, comparing normalized proportion of responding between the S+ stimuli range (D4/D#4) and both S- stimulus ranges (C4/C#4 and E4/F4). Tests of significance were corrected for family-wise error rates using Bonferroni correction ($\alpha = 0.025$). The mean proportion of response by Learners to note rangers were: C4/C#4, $M = 0.572$; D4/D#4, $M = 0.901$; and E4/F4, $M = 0.579$ [Fig. 2.2]. Learners had statistically significant differences in responding between the C4/C#4 - D4/D#4 ranges ($t_{(149)} = -21.31, p \leq 0.001$). Learners also had statistically significant differences in responding between the D4/D#4 - E4/F4 ranges ($t_{(149)} = 19.73, p \leq 0.001$).

The response trend by the Non-Learner participants suggests they did not learn to discriminate the S+ and S- ranges [Fig. 2.3]. The remaining 73 participants were identified as Non-learners. Statistical analysis was carried out using pairwise planned comparisons, comparing normalized proportion of responding between the S+ stimuli range (D4/D#4) and both S- stimulus ranges (C4/C#4 and E4/F4). Tests of significance were corrected for family-wise error using the Bonferroni correction ($\alpha = 0.025$). The mean proportion of response by Non-Learners to note ranges were: C4/C#4, $M = 0.761$; D4/D#4, $M = 0.766$; and E4/F4, $M = 0.802$. Non-learners did not show statistically significant differences in responding between the C4/C#4 - D4/D#4 ranges ($t_{(73)} = -0.213, p = 0.832$). Non-learners did not show statistically significant differences in responding between the D4/D#4 - E4/F4 ranges ($t_{(73)} = -1.871, p = 0.65$). Based on participant performance in discrimination training, all Non-Learners were excluded from any subsequent data analysis.

To examine if participants were responding differently to the 70dB and 80dB stimuli, I ran a Two-way 3 (Note range) \times 2 (dB level) ANOVA. I found an effect of note range ($F_{(2, 596)} = 368.944, p \leq 0.001$) but no interaction effect of Note range \times dB level ($F_{(2, 596)} = 0.63, p = 0.533$), suggesting there was no difference in responding based on dB level.

AP Processing Participants

Three participants identified as AP possessors [L018, DL075, and L043], and were analyzed separately from all the other participants. Individual response patterns suggest each AP possessor learned to discriminate the note ranges [Fig. 2.4]. Furthermore AP possessors

discriminated well above chance levels with AP participants correctly on 82.2% of trials compared to an average of 60.6% for Learner participants.

Generalization testing

Intra-octave Generalization testing. Response trends during Intra-octave generalization testing indicate participants did not generalize were unable to continue discrimination of the D4/D#4-E4/F4 ranges [Fig. 2.5]. Seventy-two participants were included in the Intra-octave generalization testing. The normalized proportion of responding was compared the D4/D#4 stimulus range and both of the C4/C#4 and E4/F4 note ranges, G#4/A4 stimulus range and both F#4/G4 and A#4/B4 note ranges. An omnibus repeated measures One-way ANOVA indicated a difference in responses across note ranges ($F_{(2, 70)} = 34.007, p \leq 0.001$). Tests of significance were corrected for family-wise error using the Bonferroni correction method ($\alpha = 0.013$). The mean proportion of response by participants to note ranges were: C4/C#4, $M = 0.289$, D4/D#4, $M = 0.495$; E4/F4, $M = 0.426$; F#4/G4, $M = 0.255$; G#4/A4, $M = 0.174$; and A#4/B4, $M = 0.098$. Pairwise comparisons revealed a significant difference in responding between: C4/C#4 - D4/D#4 ($t_{(71)} = 6.87, p \leq 0.001$), F#4/G4 - G#4/A4 ($t_{(71)} = 2.03, p \leq 0.001$), and G#4/A4 - A#4/B4 ($t_{(71)} = -4.35, p \leq 0.001$); and no significant difference was observed between D4/D#4 - E4/F4 ($t_{(71)} = 4.20, p = 0.047$). This trend suggests no generalization was observed. Responses to the novel note ranges was highest to F#4/G4; a decreasing response rate was observed for both G#4/A4 and A#4/B4.

Inter-octave Generalization testing. Response trends during Inter-octave generalization testing indicate that participants didn't generalize and were unable to maintain discrimination of the D4/D#4 - E4/F4 ranges [Fig. 2.6]. An omnibus repeated measures One-way ANOVA indicated a difference in responses across note ranges ($F_{(2, 70)} = 48.980, p \leq 0.001$). Seventy-two participants were included in the Inter-octave generalization testing. The normalized proportion of responding was compared between the D4/D#4 stimulus range and both of the C4/C#4 and E4/F4 note ranges, and the D5/D#5 stimulus range and both C5/C#5 and E5/F5 note ranges. Tests of significance were corrected for family-wise error using the Bonferroni correction method ($\alpha = 0.013$). The mean proportion of response by participants to note ranges were: C4/C#4, $M = 0.340$; D4/D#4, $M = 0.487$; E4/F4, $M = 0.487$; C5/C#5, $M = 0.146$; D5/D#5, $M = 0.166$; and E5/F5, $M = 0.105$. Pairwise comparisons revealed a significant difference in responding between C4/C#4 - D4/D#4 ($t_{(71)} = 5.89, p \leq 0.001$); no significant differences in responding were observed between D4/D#4 - E4/F4 ($t_{(71)} = 0.002, p = 0.998$), C5/C#5 - D5/D#5 ($t_{(71)} = 0.969, p = 0.336$), and D5/D#5 - E5/F5 ($t_{(71)} = 2.347, p = 0.022$). Responses to the novel note ranges was highest to C5/C#5 and D5/D#5; a decrease in response was observed for E5/F5. This trend for the novel note ranges suggests that the note ranges were discriminated but no generalization occurred. These results are consistent with the use of pitch height during discrimination, and not pitch chroma use.

Failure to Generalize to Novel Note Ranges

Generalization of the stimulus-response contingencies was not observed in the Intra-octave or Inter-octave conditions. The Generalization testing results are unexpected as Hoeschele et al. (2012) found generalization with a similar method. Results are consistent with the use of

pitch height as the discriminatory cue during the generalization task. Generalization of the response pattern to the F#4/G4, G#4/A4, and A#4/B4 note ranges of the Intra-octave condition would have suggested participants were transposing the learned discrimination and supported the use of an AFRS [see **Fig. 2.5**]; however, the results suggest that participants were anchoring; that is, they applied the learned discrimination across the upper range of notes (E4/F4, F#4/G4, G#4/A4, and A#4/B4). Participants responded most to the D4/D#4 and E4/F4 ranges and decreased responding as note ranges depart from the trained frequencies. Generalization was not observed in the Inter-octave condition, and a similar anchoring effect was observed with D4/D#4 and E4/F4 [see **Fig. 2.6**]. If participants had learned to discriminate the original note ranges based on pitch chroma, I would have expected to see generalization in the Inter-octave condition. It is possible that my task biased participants to discriminate based on pitch height cues rather than pitch chroma cues. Evidence to support this interpretation comes from the data provided by two AP possessors. AP possessors excel at the identification of notes based on the chromatic scale and can identify octave relationships (Miyazaki, 1988). Only one of the two AP possessors demonstrated octave equivalence [see **Fig. 2.7**], while the second AP possessor responded in a manner identical to inter-octave generalization participants. This strongly supports the suggestion participants may have been responding based on pitch height due to the expectations established during discrimination training rather than an inability to do so. The pitch height strategy participants may have learned is a low-middle-high discrimination where responses to middle frequencies are reinforced; this is supported by both the Intra-octave and Inter-octave generalization testing results.

AP possessor Inter-octave Generalization test. Fortuitously, two AP possessor participants were randomly placed in the Inter-octave Generalization test, and each responded differently to the novel note ranges. Participant L043 generalized to pitch chroma related note ranges with near perfect accuracy; while participant DL075 did not generalize at all to the novel ranges [Fig. 2.7]. This difference suggests that each participant has the ability to discriminate note ranges, but may have held different expectations for the task; participant L043 attended to pitch chroma, while participant DL075 attended to pitch height.

Transfer Testing

Intra-octave Original-transfer testing. No evidence of transfer of discrimination was observed in the F#4/G4, G#4/A4, and A#4/B4 note ranges. Results suggests participants were only able to discriminate the C4/C#4 - D4/D#4 and G#4/A4 - A#4/B4 ranges, and were unable to maintain the discrimination of note ranges learned in Discrimination training. Thirty-six participants were included in the Intra-octave original-transfer testing. The normalized proportion of responding was compared between the D4/D#4 stimulus range and both of the C4/C#4 and E4/F4 note ranges, and G#4/A4 stimulus range and both of the F#4/G4 and A#4/B4 note ranges. One-way ANOVA indicated a difference in responses across note ranges ($F_{(2, 35)} = 14.441, p \leq 0.001$) [Fig. 2.8]. Tests of significance were corrected for family-wise error using the Bonferroni correction method ($\alpha = 0.01$). The mean proportion of response by participants to note ranges were: C4/C#4, $M = 0.413$; D4/D#4, $M = 0.622$; E4/F4, $M = 0.565$; F#4/G4, $M = 0.513$; G#4/A4, $M = 0.491$; and A#4/B4, $M = 0.320$. Pairwise comparisons revealed a significant difference in responding between C4/C#4 - D4/D#4 ($t_{(35)} = 6.611, p \leq 0.001$) and G#4/A4 - A#4/B4 ($t_{(35)} = -$

0.862, $p \leq 0.001$). No significant difference in responding was observed between D4/D#4 - E4/F4 ($t_{(35)} = 5.364$, $p = 0.068$), E4/F4 - F#4/G4 ($p = 0.044$), and F#4/G4 - G#4/A4 ($t_{(35)} = -0.862$, $p \leq 0.394$).

Intra-octave Partial-reversal Transfer. No evidence of AFRS use was observed in the F#4/G4, G#4/A4, and A#4/B4 note ranges. Results suggest participants were only able to discriminate the C4/C#4 - D4/D#4 note range, and were unable to discriminate any other note range during Transfer testing. Thirty-six participants were included in the Intra-octave reversal-transfer testing. The normalized proportion of responding was compared between the D4/D#4 stimulus range and both of the C4/C#4 and E4/F4 note ranges, and G#4/A4 stimulus range and both of the F#4/G4 and A#4/B4 note ranges. One-way ANOVA indicated a difference in responses across note ranges ($F_{(2, 35)} = 4.452$, $p = 0.012$) [**Fig. 2.9**]. Tests of significance were corrected for family-wise error using the Bonferroni correction method ($\alpha = 0.01$). The mean proportion of response by participants to note ranges were: C4/C#4, $M = 0.599$; D4/D#4, $M = 0.565$; E4/F4, $M = 0.599$; F#4/G4, $M = 0.576$; G#4/A4, $M = 0.611$; and A#4/B4, $M = 0.576$. Pairwise comparisons revealed a significant difference in responding between C4/C#4 - D4/D#4 ($t_{(35)} = -5.427$, $p \leq 0.001$). No significant difference in responding was observed between D4/D#4 - E4/F4 ($t_{(35)} = -0.825$, $p = 0.415$), E4/F4 - F#4/G4 ($t_{(35)} = -1.251$, $p \leq 0.220$), F#4/G4 - G#4/A4 ($t_{(35)} = 1.311$, $p \leq 0.199$), and G#4/A4 - A#4/B4 ($t_{(35)} = 0.988$, $p \leq 0.330$). AFRS use would have lead to transfer in this condition, since the response contingencies are congruent with the pattern predicted by AFRS, e.i., S-/S+/S-/S+/S-/S+.

Inter-octave Original-transfer testing. Evidence of transfer was observed in the Inter-octave Original-transfer condition. Response trends suggest that participants were able to discriminate all note ranges in a manner consistent with pitch chroma perception. Thirty-six participants were included in the Inter-octave original-transfer testing. The normalized proportion of responding was compared between the D4/D#4 stimulus range and both of the C4/C#4 and E4/F4 note ranges; D5/D#5 stimulus range and both of the C5/C#5 and E5/F5 note ranges. One-way ANOVA indicated a difference in responses across note ranges ($F_{(2, 35)} = 10.058, p \leq 0.001$) [Fig. 2.10]. Tests of significance were corrected for family-wise error using the Bonferroni correction method ($\alpha = 0.013$). The mean proportion of response by participants to note ranges were: C4/C#4, $M = 0.451$; D4/D#4, $M = 0.660$; E4/F4, $M = 0.532$; C5/C#5, $M = 0.358$; D5/D#5, $M = 0.480$; and E5/F5, $M = 0.363$. Pairwise comparisons revealed a significant difference in responding between C4/C#4 - D4/D#4 ($t_{(35)} = -5.795, p \leq 0.001$), D4/D#4 - E4/F4 ($t_{(35)} = 3.200, p = 0.003$), C5/C#5 - D5/D#5 ($t_{(35)} = -3.538, p = 0.001$), and D5/D#5 - E5/F5 ($t_{(35)} = 3.200, p = 0.003$). This is pattern of responding is consistent with predictions for pitch chroma use.

Inter-octave Partial-reversal Transfer testing. No evidence for transfer was observed, but evidence for pitch chroma use was observed. Response trends suggest that participants were unable to discriminate all note ranges in a manner consistent with pitch chroma perception. Thirty-six participants were included in the Inter-octave original-transfer testing. The normalized proportion of responding was compared between the D4/D#4 stimulus range and both of the C4/C#4 and E4/F4 note ranges; D5/D#5 stimulus range and both of the C5/C#5 and E5/F5 note ranges. One-way ANOVA indicated no difference in responses across note ranges ($F_{(2, 35)} =$

2.079, $p = 0.568$) [Fig. 2.11]. The mean proportion of response by participants to note ranges were: C4/C#4, $M = 0.447$; D4/D#4, $M = 0.517$; E4/F4, $M = 0.488$; C5/C#5, $M = 0.498$; D5/D#5, $M = 0.521$; and E5/F5, $M = 0.507$. The omnibus repeated-measures ANOVA was not significant after correction, therefore no pairwise comparisons were carried out. Participants were unable to discriminate the any of the note ranges. This is pattern of responding is congruent with predictions for pitch chroma use during the discrimination task.

Category Perception of Pitch Chroma in Transfer Testing

Generalization testing results did not suggest participants were discriminating based on pitch chroma, but transfer testing did support pitch chroma based discrimination. I observed successful discrimination of all note ranges in the Inter-octave Original-transfer condition [see Fig 2.10], an improvement when compared to Inter-octave generalization [see Fig 2.6]. If participants in the Inter-octave original-transfer condition had learned to respond based feedback from Transfer testing, then I would expect to see similar learning of response patterns in the Intra-octave original-transfer condition [see Fig 2.7]. Results suggest that the response contingencies may have facilitated the discrimination of note ranges in the Inter-octave Original-transfer condition. The Inter-octave partial-reversal condition results further support the use of pitch chroma cues by the participants [see Fig 2.11]. Participants were able to differentiate the C4-F4 and C5-F5 note ranges in Generalization testing based on pitch height, but were unable to discriminate these notes in the Inter-octave Partial-reversal condition. This suggests the partial reversal of response contingencies resulted an interference effect as predicted if the participants perceive pitch chroma related notes as a perceptual category.

Conclusion

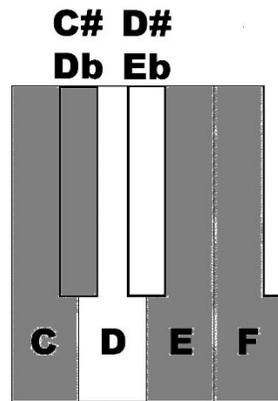
In Experiment 1 I found that participants' pattern of responding did not generalize between discrimination training and generalization testing. Participants were provided with minimal instruction allowing them to construct their own behavioural rules for the task. Overall, participants seemed to respond using a pitch height rather than pitch chroma strategy. During transfer testing, I found participants were unable to learn the response contingencies for the Intra-octave original-transfer condition and Intra-octave partial-reversal condition. I also found that participants learned response contingencies for the Inter-octave original-transfer condition; furthermore, participant performance declined in the Inter-octave partial-reversal condition, suggesting that the opposing response contingencies of pitch chroma matched notes (e.g., C4 and C5) was responsible for the decline in performance and indicates the participants were perceiving pitch chroma related notes as a perceptual category.

Tables & Figures

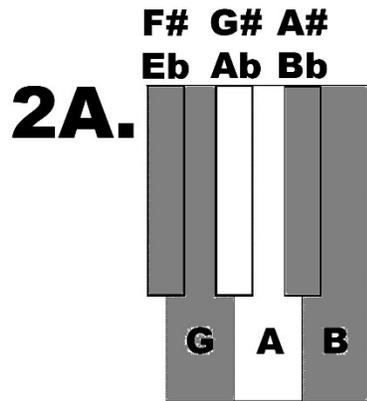
Figure.2.1. Transfer testing response contingencies

Figure.2.1. Depicts the response contingencies for notes during Transfer testing. 1. Depicts the response contingencies for notes C4-F4 for all conditions. Grey indicates S- notes, while white indicates S+ notes. 2A. Depicts the response contingencies for notes F#4-B4 for the Intra-octave Original-transfer condition. 2B. Depicts the response contingencies for notes F#4-B4 for the Intra-octave Partial-reversal condition. 2C. Depicts the response contingencies for notes C5-F5 for the Intra-octave Original-transfer condition. 2D. Depicts the response contingencies for notes C5-F5 for the Intra-octave Partial-reversal condition.

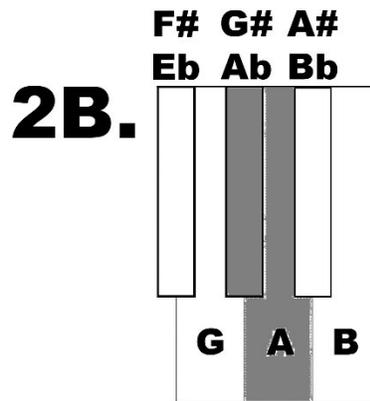
1. Octave 4



Intra-octave
Octave 4

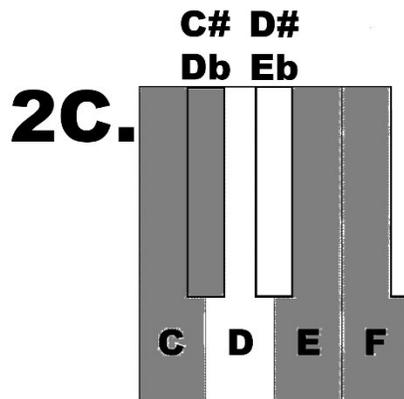


Original-transfer

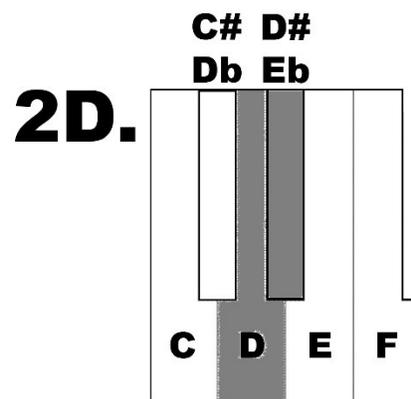


Partial-reversal

Inter-octave
Octave 5



Original-transfer



Partial-reversal

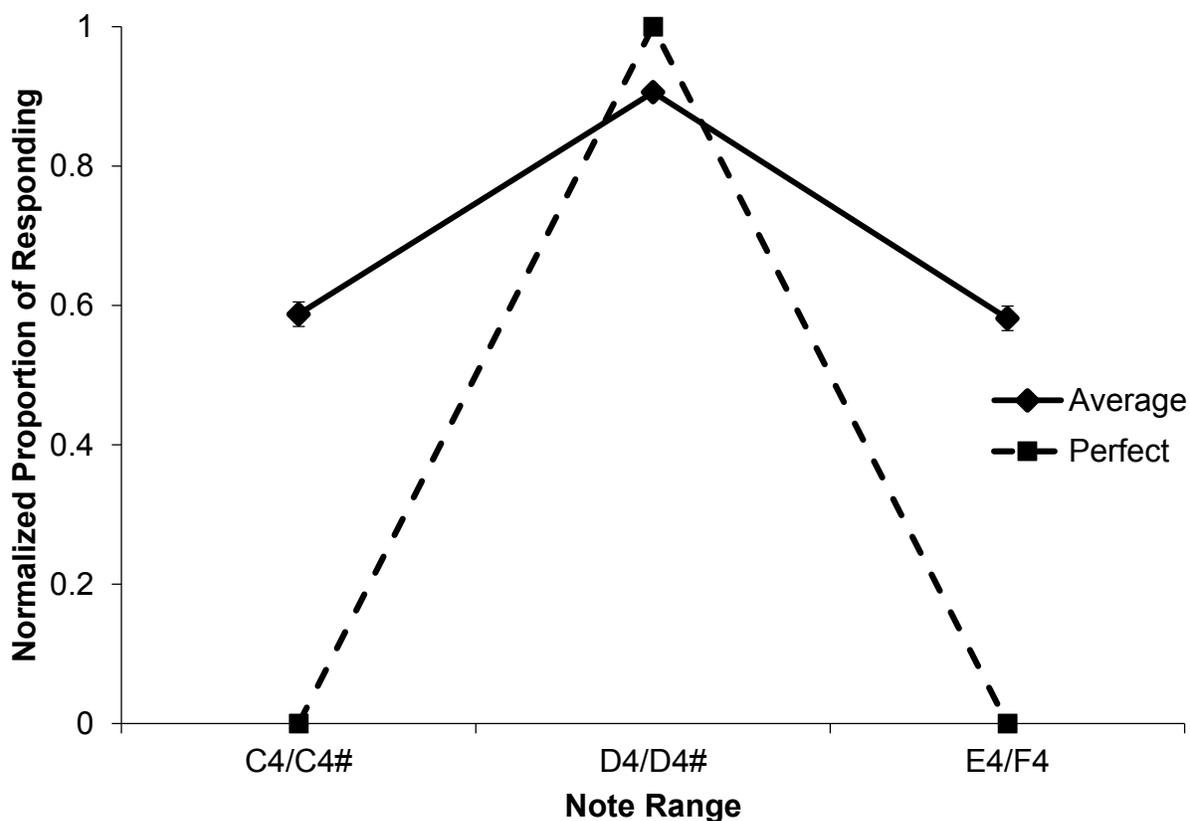
Figure 2.2. Learner Discrimination training

Figure 2.2. Learner Discrimination training. Graph depicts the normalized average proportion of responding during Discrimination training for Learner participants. S+ stimuli range D4/D#4 and S- stimulus ranges C4/C#4 and E4/F4. Solid line indicates the average group response for participants. Dashed line indicates the expected response if participants were perfectly accurate. Error bars are \pm S.E.M.

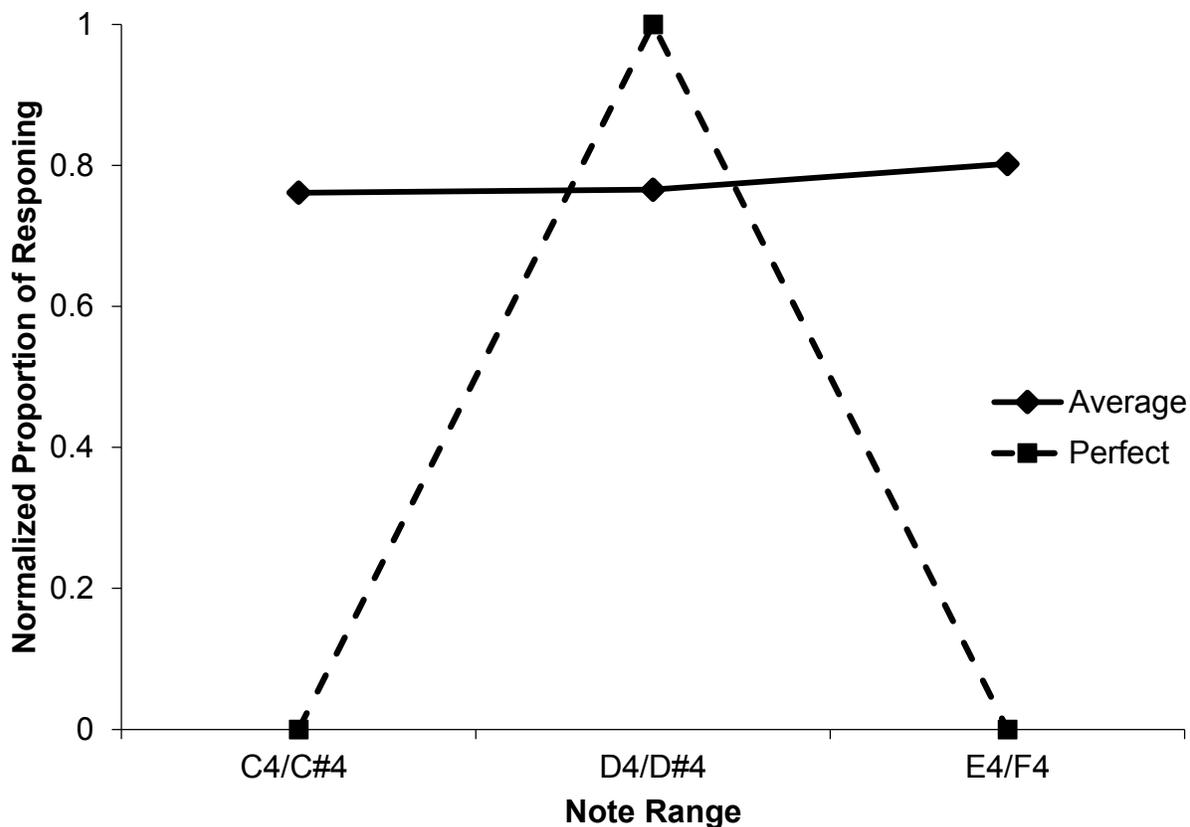
Figure 2.3. Non-Learner Discrimination training

Figure 2.3. Non-Learner Discrimination training. Graph depicts the normalized average proportion of responding during Discrimination training for Non-Learner participants. S+ stimuli range D4/D#4 and S- stimulus ranges C4/C#4 and E4/F4. Solid line indicates the average group response for participants. Dashed line indicates the expected response if participants were perfectly accurate. Error bars are \pm S.E.M.

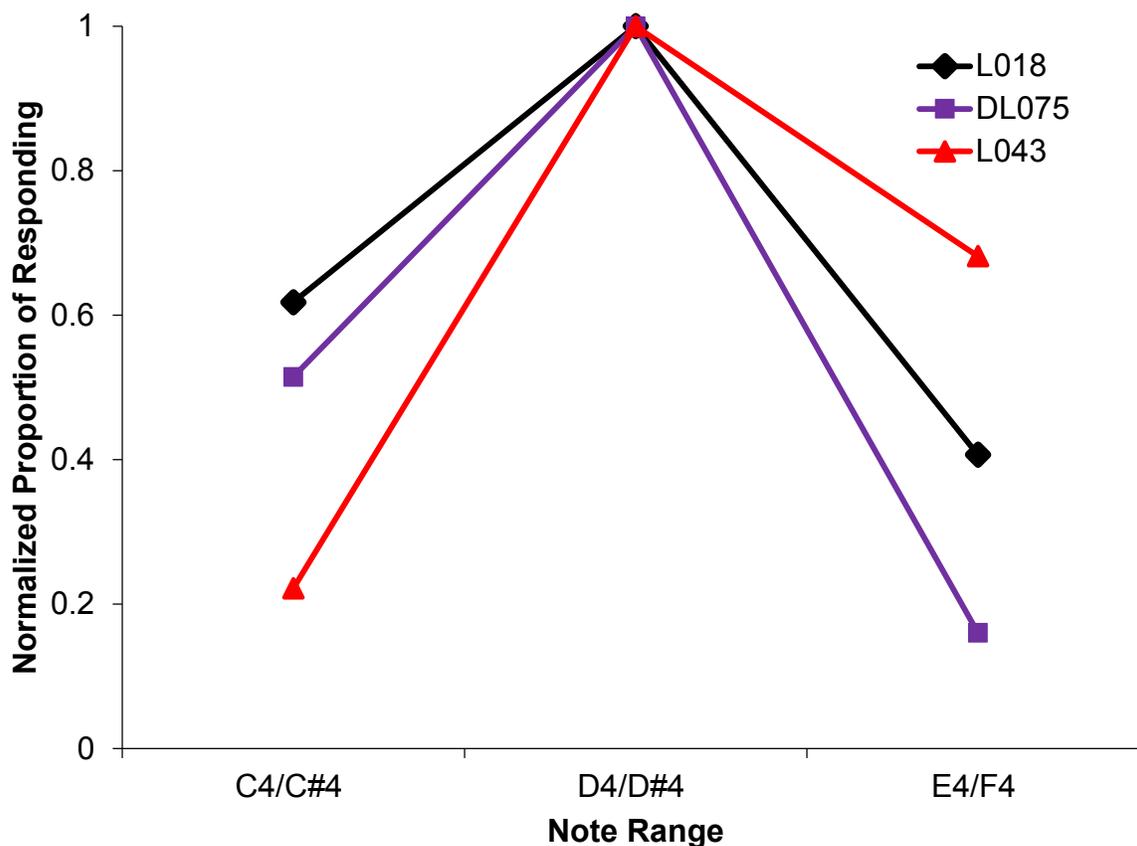
Figure 2.4. AP possessor Discrimination training

Figure 2.4. AP possessor Discrimination training. Graph depicts the normalized average proportion of responding during Discrimination training for AP possessor participants. S+ stimuli range D4/D#4 and S- stimulus ranges C4/C#4 and E4/F4. Solid line indicates the average group response for participants. Dashed line indicates the expected response if participants were perfectly accurate. Error bars are \pm S.E.M.

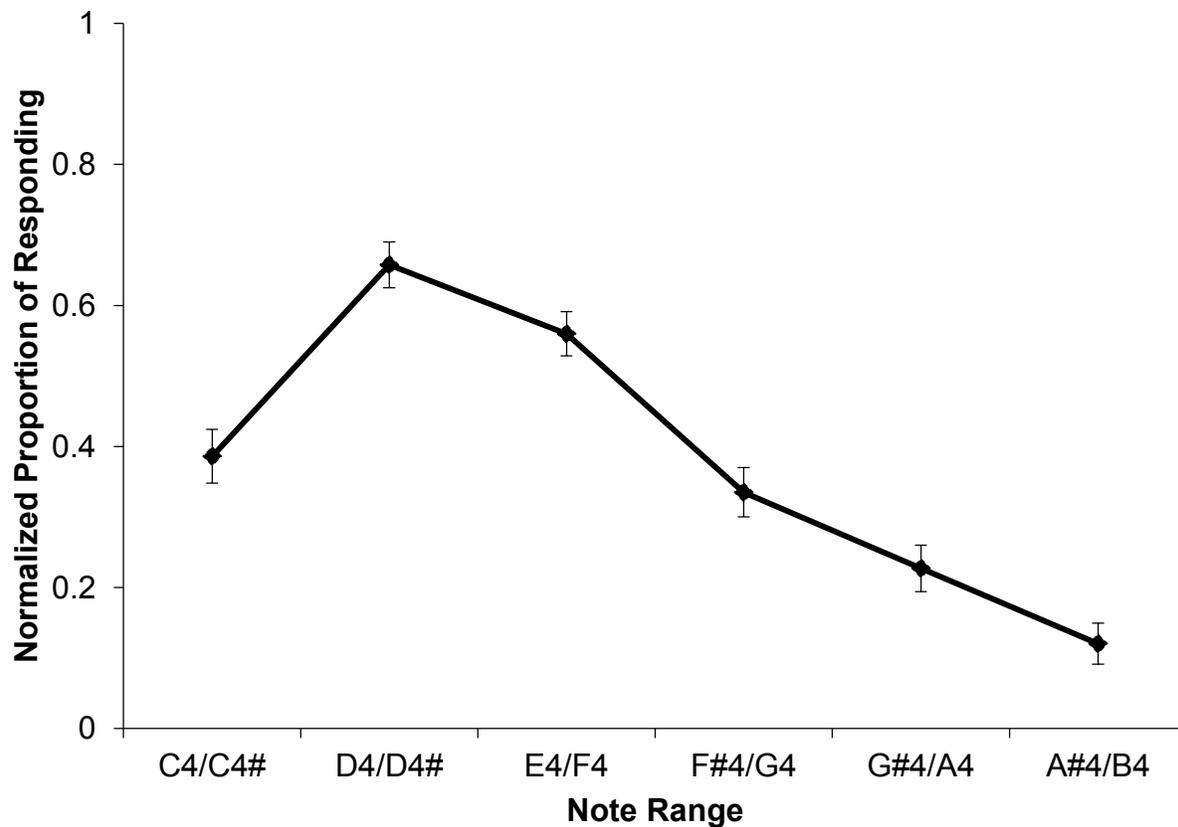
Figure 2.5. Intra-octave Generalization testing

Figure 2.5. Intra-octave Generalization testing. Graph depicts the normalized average proportion of responding during Generalization testing for Learner participants to six note pairs from the 4th octave. Solid line indicates the average group response for participants. Error bars are \pm S.E.M.

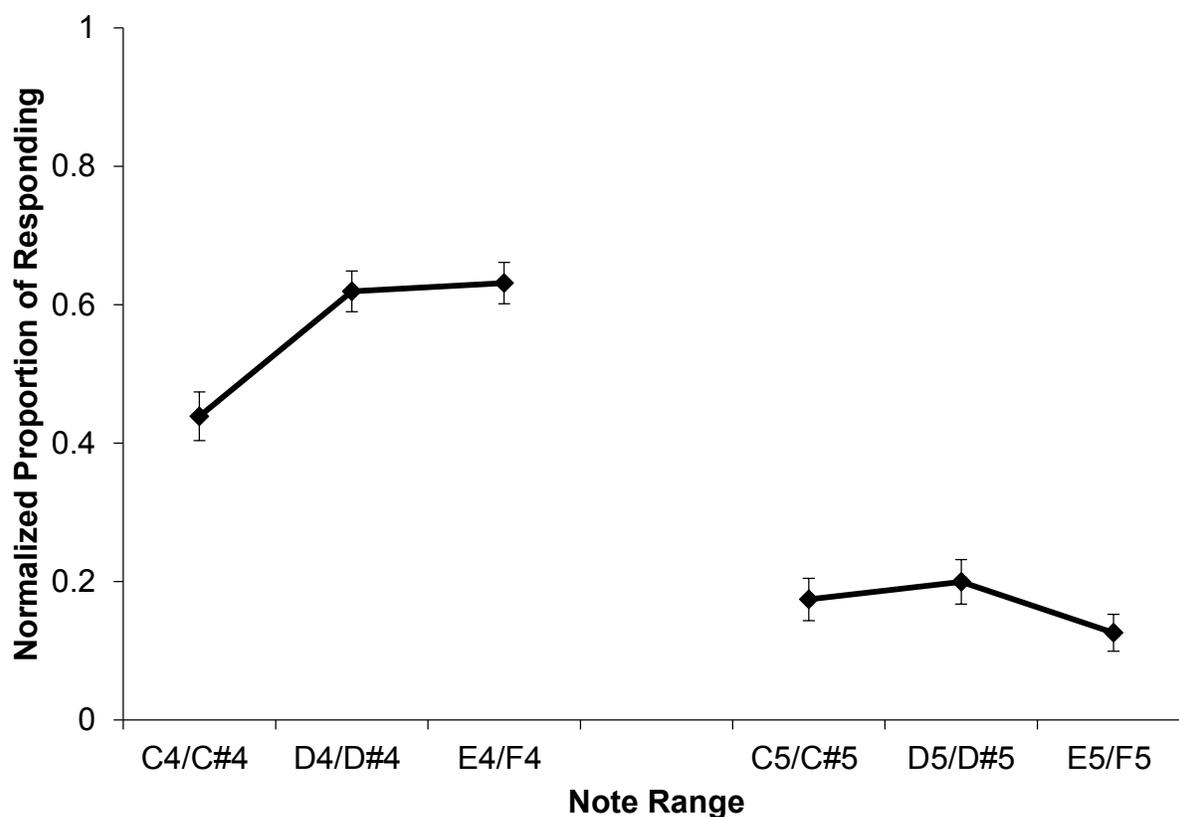
Figure 2.6. Inter-octave Generalization testing

Figure 2.6. Inter-octave Generalization testing. Graph depicts the normalized average proportion of responding during Generalization testing for Learner participants to three note pairs from the 4th octave and three note pairs from the 5th octave. Solid line indicates the average group response for participants. Error bars are \pm S.E.M.

Figure 2.7. AP possessor Inter-octave Generalization test

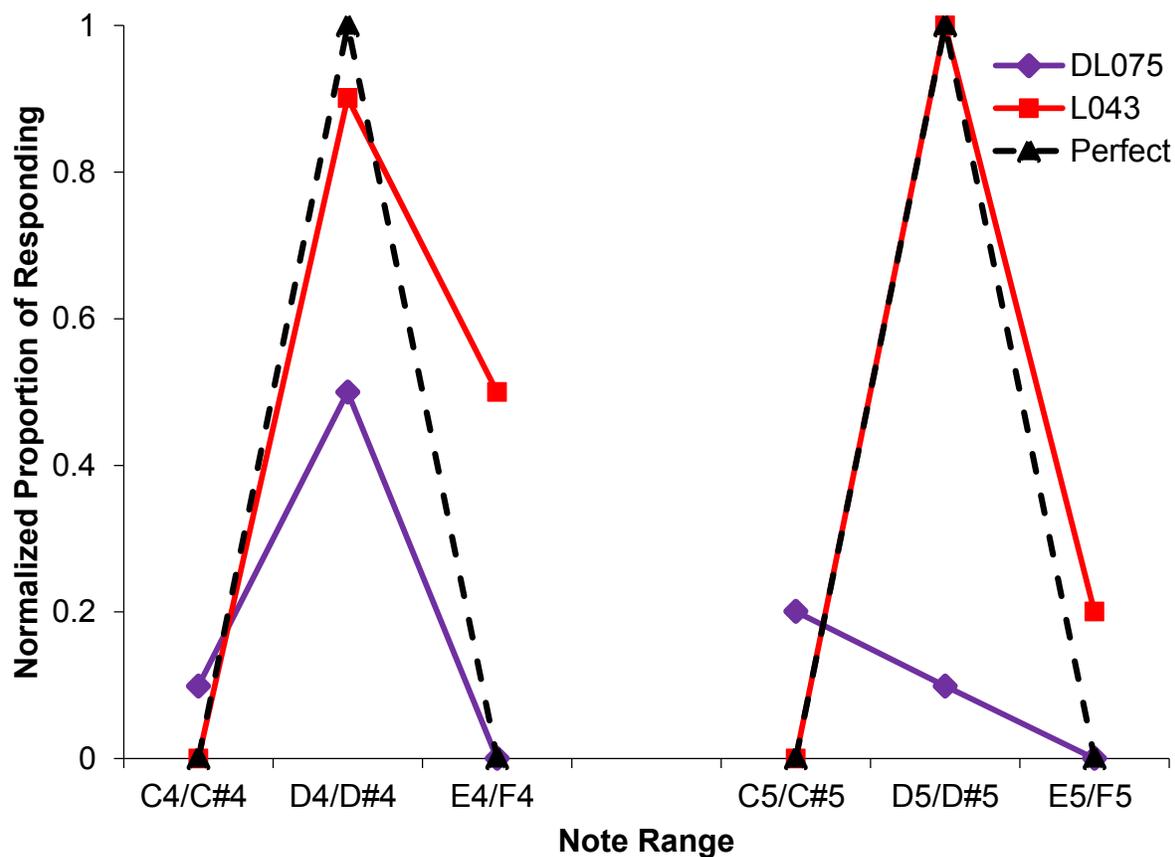


Figure 2.7. AP possessor Inter-octave Generalization test. Participants normalized average proportion of responding during a generalization task for AP possessor participants. Dashed line indicates expected responding based on perfect discrimination and generalization. Error bars are \pm S.E.M.

Figure 2.8. Intra-octave Original-transfer testing

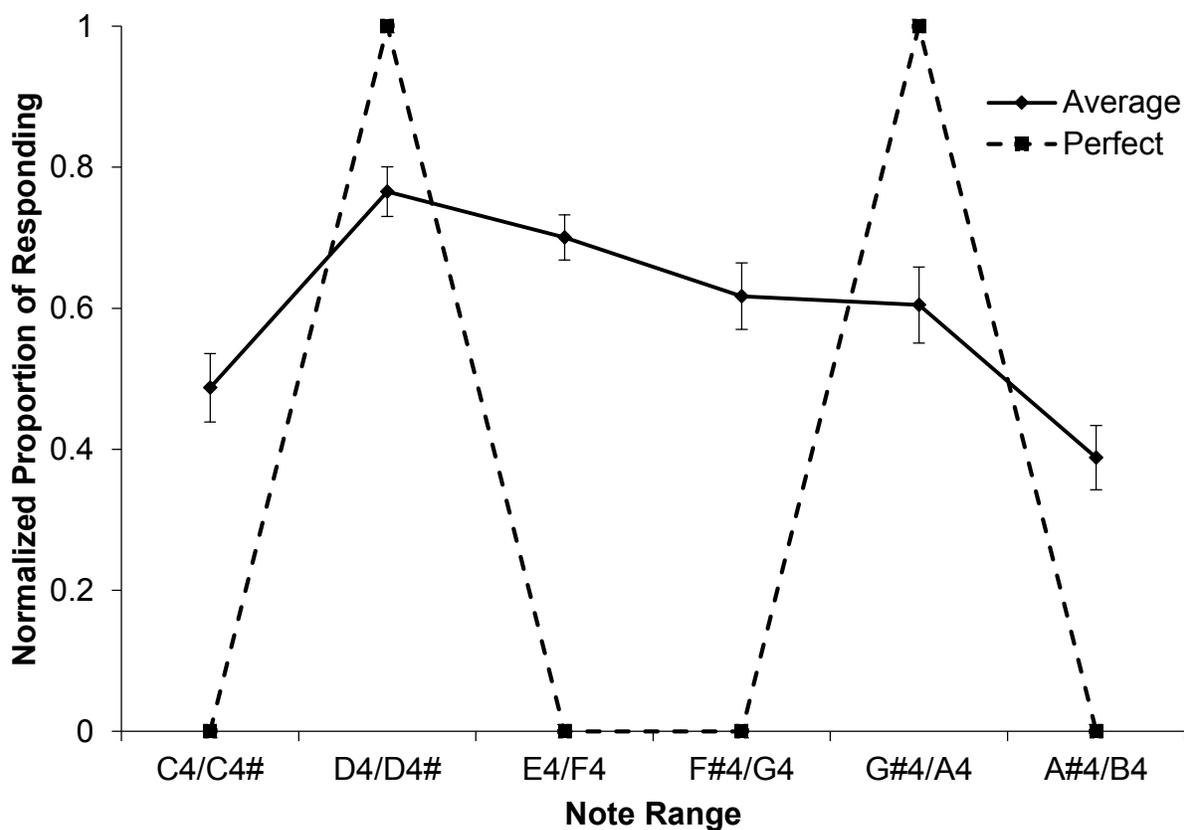


Figure 2.8. Intra-octave Original-transfer testing. Participants normalized average proportion of responding during Transfer testing for Intra-octave original-transfer participants. S+ ranges: D4/D#4 and G#4/A4. S- Ranges: C4/C#4, E4/F4, F#4/G4, and A#4/B4. Solid line indicates the average group response. Dashed line indicates expected responding based on perfect discrimination. Error bars are \pm S.E.M.

Figure 2.9. Intra-octave Partial-reversal Transfer testing

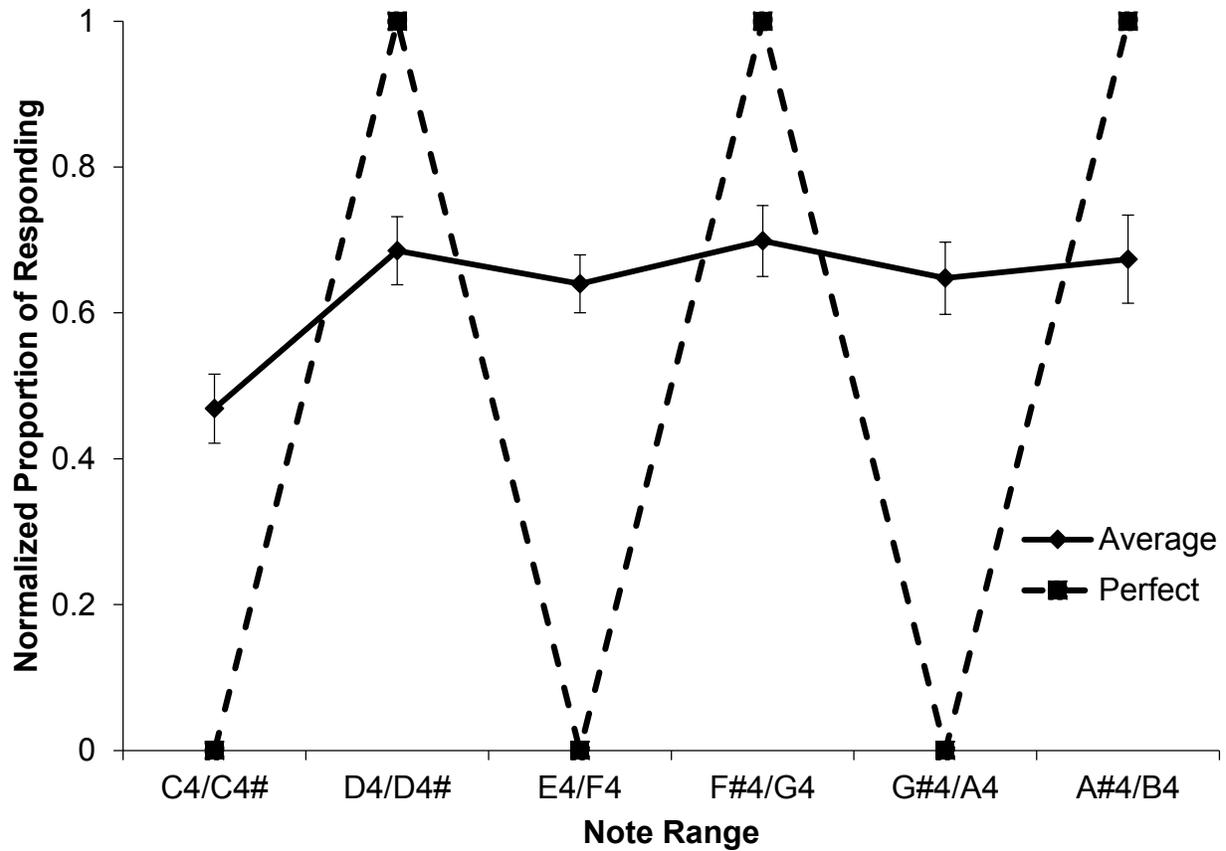


Figure 2.9. Intra-octave Partial-reversal Transfer testing. Participants normalized average proportion of responding during Transfer testing for Intra-octave Partial-reversal participants. S+ ranges: D4/D#4, F#4/G4, and A#4/B4. S- Ranges: C4/C#4, E4/F4, and G#4/A4. Dashed line indicates expected responding based on perfect discrimination. Solid line indicates the average group response. Error bars are \pm S.E.M.

Figure 2.10. Inter-octave Original-transfer testing

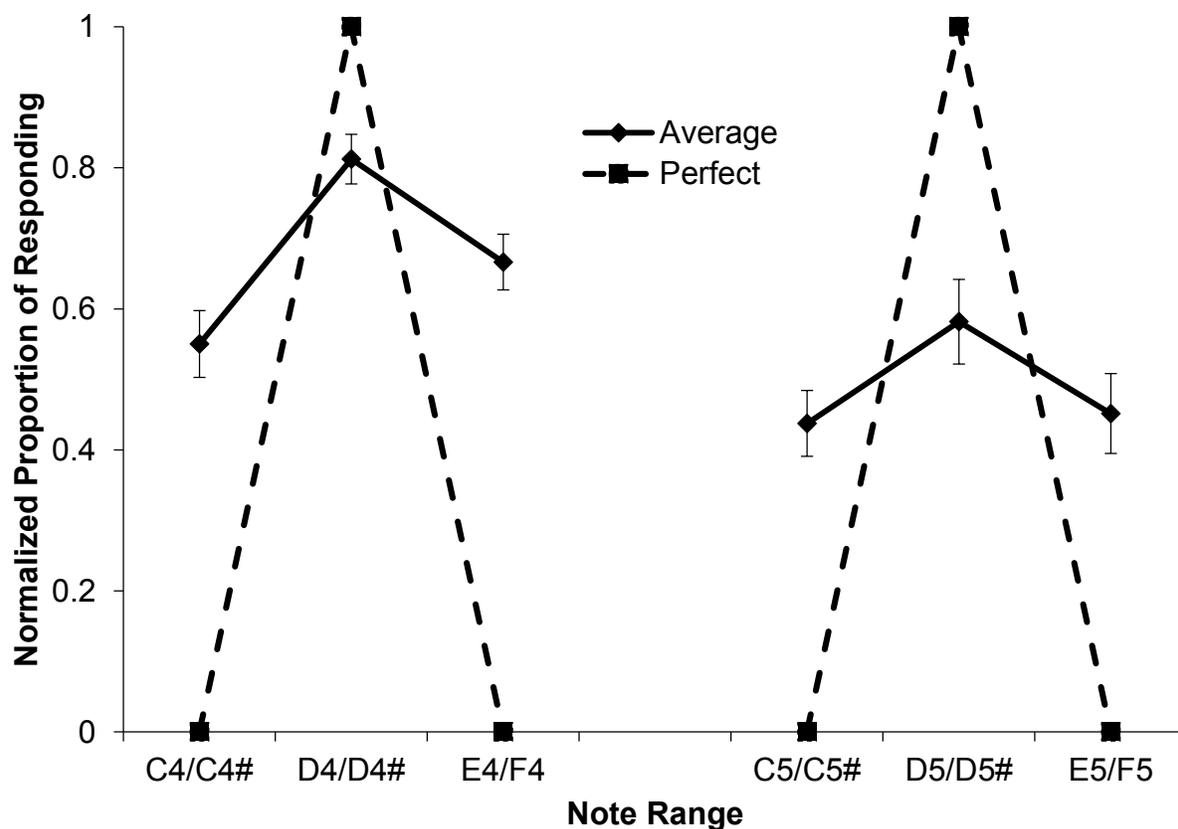


Figure 2.10. Inter-octave Original-transfer testing. Participants normalized average proportion of responding during Transfer testing for Inter-octave original-transfer participants. S+ ranges: D4/D#4 and D5/D#5. S- ranges: C4/C#4, E4/F4, C5/C#5, and E5/F5. Dashed line indicates expected responding based on perfect discrimination. Solid line indicates the average group response. Error bars are \pm S.E.M.

Figure 2.11. Inter-octave Partial-reversal Transfer testing

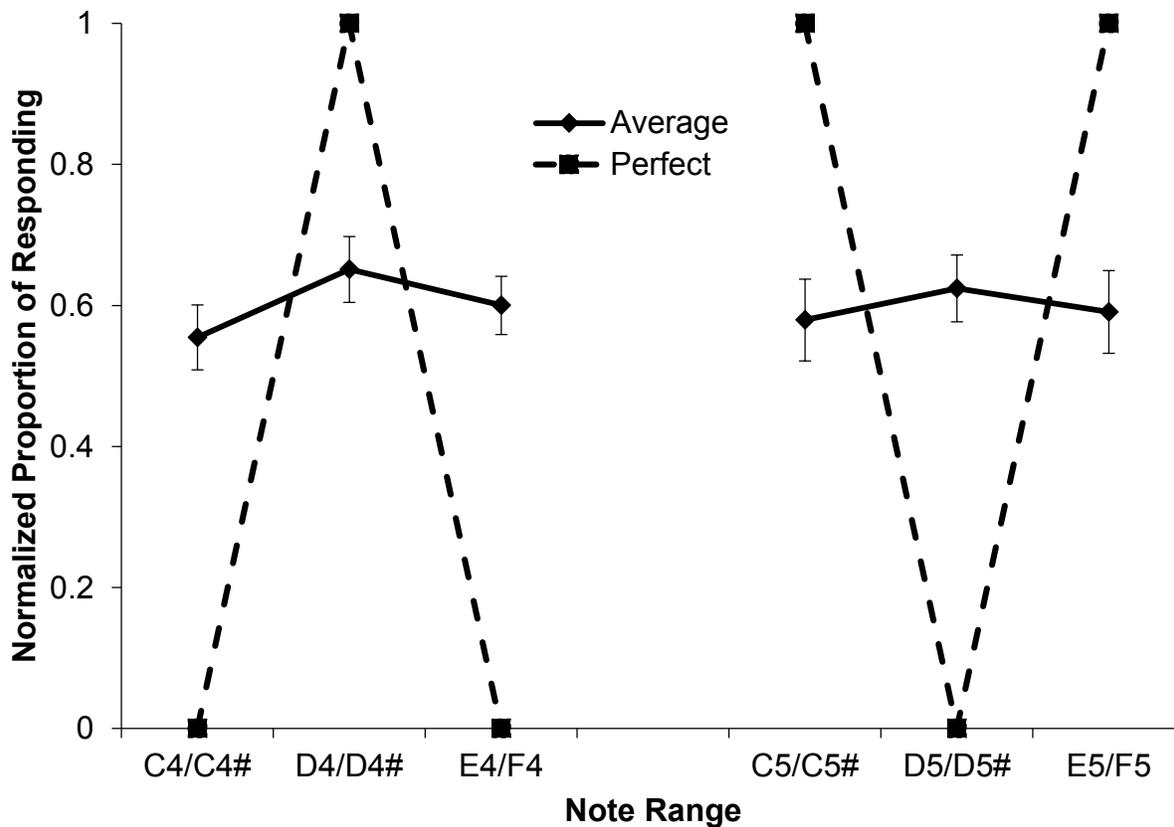


Figure 2.11. Inter-octave Partial-reversal Transfer testing. Participants normalized average proportion of responding during Transfer testing for Inter-octave Partial-reversal Transfer participants. S+ ranges: D4/D#4, C5/C#5, and E5/F5. S- ranges: C4/C#4, E4/F4, and D5/D#5. Dashed line indicates expected responding based on perfect discrimination. Solid line indicates the average group response. Error bars are \pm S.E.M.

Chapter 3: Introduction (Experiment 2)

Chickadees have exceptional AP perception and their auditory perception is far more acute than the average human (Weisman et al., 2010). In an auditory go/no-go discrimination experiment, boreal chickadees (*Poecile hudsonicus*) and humans were presented with a series of 40 tones, and were required to discriminate alternating ranges of 5 tones (e.g., S+/S-/S+/S-/S+). Boreal chickadees and AP possessor humans were able to learn the discrimination after multiple training sessions; non-AP possessors were unable to discriminate the note ranges. In an experiment by MacDougall-Shackleton and Hulse (1996), European starlings were required to discriminate a sequence of tones based on AP or RP and found that the use of RP was highly constrained by the use of AP. In line with previous results, it is possible that chickadees would show a preference or reliance on pitch height perception and fail to express pitch chroma perception.

The purpose of Experiment 2 was to ascertain if chickadees could perceive octave equivalence. In a previous experiment, Hoeschele et al. (2013) concluded that chickadees had either not been able to perceive pitch chroma or used an AFRS, meaning that, through training, the subjects had learned that S- ranges were followed by S+ ranges and vice versa. Hoeschele et al. (2013) did not conclusively rule out pitch chroma perception in chickadees. The goal of Experiment 2 was to examine if the chickadees learned an AFRS and whether chickadees perceived the perceptual categories of pitch chroma.

Methods (Experiment 2)

Subjects. Twenty-eight wild caught black capped chickadees (12 female, 16 male as identified by DNA analysis) were tested between July 2014 and July 2015. These birds were captured from Barrier Lake Field Station in Kananaskis Country, Alberta, Canada (51.02°N, 115.03°W), or in and around Edmonton, Alberta, Canada (Stony Plain, 53.46°N, 114.01°W; North Saskatchewan River Valley, 53.53°N, 113.53°W; Mill Creek Ravine, 53.52°N, 113.47°W), between December 2010 and February 2013. Experimental protocols were approved by the Animal Care and Use Committee – Biosciences at the University of Alberta.

Chickadees were maintained on a light/dark cycle that followed natural light cycle for Edmonton, Alberta, Canada. Each chickadee had prior experience with operant discrimination tasks, but was naïve to the current stimulus set. Twelve birds were removed from the experiment at various stages of the experiment due to health concerns (two birds had feeding rates $\leq 15\%$) or failure to meet training criteria after an extended period of time.

Birds were housed individually in Jupiter Parakeet cages (30 × 40 × 40 cm, Rolf C. Hagen, Inc., Montreal, Canada) in colony rooms. Birds did not have physical contact with one another but did have visual and auditory contact. Birds had *ad libitum* access to food (Mazuri Small Bird Maintenance Diet; Mazuri, St Louis, MO, USA), water, Prime vitamin supplement (Hagen, Inc., Montreal, Canada), grit, and cuttlebone. Birds were given a mixture of spinach or parsley and eggs twice a week, a small number of sunflower seeds daily, and one superworm (*Zophobas morio*) three times a week.

Apparatus

During the experiment, birds were housed in modified colony-room cages. Each cage was placed inside a ventilated chamber lined with sound attenuating acoustic foam. Birds had *ad libitum* access to cuttlebone, water and grit. The chambers were illuminated by a 9-W, full spectrum fluorescent bulb 6500K 9W bulbs (TCP, Inc., Aurora, Ohio, United States). A cage opening (11 × 16 cm) gave each bird access to a motor-driven feeder (Njegovan et al., 1994). Infrared detectors on the feeder and the request perch monitored the position of the bird during a trial. Each operant chamber was connected to a computer and an EC single board computer (Palya & Walter, 2001) which scheduled trials, selected auditory stimuli, and recorded responses to stimuli. Stimuli were played from a Creative Sound Blaster X-Fi Xtreme audio PCI express soundcard (108 dB signal to noise ratio) through either a Cambridge A660 Integrated Amplifier (Cambridge Audio, London, England), a Cambridge A300 Integrated Amplifier (Cambridge Audio, London, England) or a NAD310 Integrated Amplifier (NAD Electronics, London, England). Auditory stimuli were emitted from a Fostex FE108 full-range speaker (Fostex Corp., Japan; frequency range 200–16,000 Hz) located to the left of the feeder; see Sturdy and Weisman (2006) for a more detailed description of the apparatus.

Stimuli

Stimuli used in Experiment 2 were the identical sound files to those used in Experiment 1. Refer to Experiment 1 for stimuli details. Sound in each operant chamber was adjusted to emit each stimulus at the intended 70dB or 80dB.

Procedure

Each bird progressed successively through *Pre-training*, *Discrimination training*, *Pre-testing*, *Generalization testing*, *Transfer testing*, and *Transfer Discrimination training* as described in the following sections [Table 3.1].

Pre-training. Birds ($n = 28$) were pre-trained and conditioned to obtain food from an automated feeder by responding to an auditory stimulus following the stages outlined, below.

Shaping. All birds were trained in successive steps to activate the feeder by landing on a request perch and landing in the feeder apparatus to gain access to food. Birds were then trained to activate an auditory stimulus by landing on the request perch and respond only to a 1-s, 1,000 Hz sine wave tone. Subjects were required to discriminate the 1,000 Hz tone from silence when initiating a trial sequence. Once a bird had reached a $DR \geq 80\%$, Non-differentiation training began. Five birds were removed from the experiment after 20,000 trials due to failure to discriminate the tone from silence to a criteria of $DR \geq 80\%$.

Non-differential training. Birds' ($n = 23$) responses were reinforced with 1 s access to food for responding on every trial to a stimulus presentation; of all 36 tones (12 notes from the 4th octave and the first six notes of the 5th octave at 70 dB and 80 dB) were presented during this training stage. A trial began when a bird landed on the request perch and remained for 900-1100ms. A tone was then selected randomly without replacement and presented once. If the bird left the

perch before the stimulus had completed playing, the house light was turned off for 30 seconds; the trial was considered incomplete and not counted towards learning criteria. If the bird left the perch and entered the feeder within 1 s of stimulus offset, then the bird was provided with 1 s of food access, followed by a 30-s lit inter-trial interval (ITI). If the subject remained on the perch after stimulus offset, an ITI of 60 s was used. During this time, the bird could initiate another trial by leaving the request perch and returning; doing so ended the ITI. This was done to promote high rates of response on every trial. Birds remained on non-differentiation training until they consistently maintained high feeding rates as determined by three criterion: either 6 blocks of $\geq 60\%$ feeding or (for two birds) 6 pairs of consecutive blocks of $\geq 30\%$ feeding (responding to $\geq 60\%$ of trials in 720 trial blocks or responding at $\geq 30\%$ in 12 blocks), 4 blocks of $\leq 3\%$ difference in responding to future discrimination tones, and 4 blocks of $\leq 3\%$ difference in responding to future generalization tones. Two birds were removed from the experiment at this stage because they were feeding on less than 15% of all trials. Two birds were removed from the experiment due to failure to meet feeding criteria after extensive training (40,000 trials).

Discrimination training. Birds ($n = 19$) were then moved on to Discrimination training, each individual trial was similar to Non-differential training except that only 6 notes were presented (C4, C#4, D4, D#4, E4, and F4 at 70 dB and 80 dB). Responses following either D4 or D#4 was rewarded (S+) with 1 s of access to food while responses to C4, C#4, E4, F4 were not rewarded (S-). Responses to S- tones resulted in a 30-s ITI with the house light out. Discrimination training was continued until each bird completed 6 blocks (480 trials) at $\geq 80\%$ DR with the last two blocks consecutive. Three birds were removed from the experiment at this stage due to failure to

meet training criterion in any block of discrimination training after extensive training (40,000 trials). One bird met training criteria on 6 blocks of training after 35,000 trials but did not meet the last two consecutive-blocks criteria and experienced a total of 85,000 trials. This bird was moved on to Pre-testing without meeting the last two consecutive-blocks criteria and was part of the Intra-octave partial reversal group.

Pre-testing. After completing Discrimination training, birds ($n = 16$, 8 male and 8 female) were moved on to Pre-testing. This training phase was identical to Discrimination training except that responses to S+ tones were only reinforced on 85% of trials. On unrewarded S+ trials the ITI was 30 s with the house light on, but no access to food was given. Intermittent reward was provided to prepare for the unrewarded test trials during Generalization testing. Birds remained on Pre-testing until they reached $DR \geq 0.80$ on two consecutive blocks (480 trials).

Generalization testing. This testing phase was similar to Pre-testing except that I introduced six notes and test tones were never reinforced. Birds were randomly assigned into two groups: Intra-octave and Inter-octave [**Table 3.1**]. Group membership determined which novel tones were introduced in Generalization testing: test notes F#4, G4, G#4, A4, A4#, and B4 for the Intra-octave group ($n = 8$, 4 male and 4 female); and C5, C#5, D5, D#5, E5, and F5 for the Inter-octave group ($n = 8$, 4 male and 4 female). Notes from Discrimination training were presented 20 times in a block at 70dB and 80dB, and each novel tone was presented once in each block for a total of 246 trials.

To address the confound of pitch and loudness during Generalization testing each bird heard half of the novel notes at 70 dB and half at 80 dB on any given block. This was counterbalanced within-group so that half the birds of each sex received each version of the test first. Birds continued on Generalization testing until they had completed at least three blocks of each test version. Generalization testing was repeated twice so that each bird heard all six notes at both dB levels. Subjects were required to complete 1 block of Pre-testing at $DR \geq 0.80$ before completing Generalization testing a second time.

Transfer testing. After Generalization testing, birds were required to complete at least one block of discrimination training with $DR \geq 0.80$ before moving on to transfer testing. Transfer testing was similar to Generalization testing except that responding to Intra-octave and Inter-octave tones was reinforced. Birds were divided into two sub-conditions ($n = 4$, 2 male and 2 female, for each sub-condition): the Original-transfer condition, and the Partial-reversal transfer condition. This was done for birds in both Intra-octave and Inter-octave condition [**Table 3.1**]. Both the Original-transfer condition and Partial-reversal condition were rewarded for responses to the middle pair (D4/D#4) while the lower frequency pair (C4/C#4) and higher frequency pair (E4/F4) of Discrimination training notes were not rewarded. These reinforcement contingencies were maintained in the Original-transfer condition for the transfer tones (Intra-octave or Inter-octave), such that responses to the middle pair of notes were reinforced and responses to the lowest and highest frequency pair of notes were not reinforced. These reinforcement contingencies were opposite for the Partial-reversal condition, such that responses to the lowest and highest frequency pairs of transfer notes were rewarded while responses to the middle pair of

transfer notes were not rewarded. Transfer testing was continued until each bird completed six blocks (480 trials) at $\geq 80\%$ DR to transfer tones, with the last two blocks consecutive, or completed 20 blocks of Transfer of training.

Transfer Discrimination training. After Transfer testing, birds ($n=16$, 8 male and 8 female) completed Transfer Discrimination training if they did not respond to Intra-octave or Inter-octave tones at a significant rate ($\leq 10\%$) in any of the 20 blocks or did not meet the Transfer training criteria in any block. The goal of Transfer Discrimination training was to examine if birds had learned, but previously failed to demonstrate, discrimination of transfer tones. Transfer Discrimination training was conducted by presenting only Intra-octave or Inter-octave tones at 70 dB and 80dB 20 times in each block (480 trials). Reward contingencies for go responses remained the same for each bird between Transfer training and Transfer Discrimination training (e.g., if a bird in the Intra-octave Original-transfer discrimination condition was rewarded for go responses to D4/D#4 and G#4/A4 in Transfer Discrimination training, then go responses to G#4/A4 were rewarded in Transfer Discrimination training). Birds continued on Transfer Discrimination training until each bird completed 6 blocks at $\geq 80\%$ DR with the last two blocks consecutive or to an individualized maximum. One bird in the Inter-octave Original-transfer condition met training criterion. For all birds the individualized maximum was determined by the number of blocks each bird required to meet criterion in Discrimination training plus five blocks of trials (e.g., a bird that meet learning criterion in Discrimination training after 40 blocks would be given up to 45 blocks of training in Transfer training).

Response Measures. Due to the large variation in the overall response rates by each individual, I report the individually normalized and group averaged percent of response across each note or note range. The averaging of raw scores would have resulted in data non-representative of responses made by each individual. Normalization was accomplished by determining a bird's highest response rate to all notes, and using this number to normalize (e.g., responses to C4 = 0.8, C4# = 0.6, and D4 = 0.2; normalization would result in values of C4 = 1.0, C4# = 0.75, and D4 = 0.25).

To determine when birds successfully learned to discriminate S+ note ranges from S- note ranges, I calculated a discrimination ratio (DR) for each block of training. The DR is a standard measure that falls between 0 and 1, where 0 means all visits to the feeder were responses to S- notes, 0.5 represents indifferent responding to S+ and S- notes, and 1.0 represents perfect discrimination of S+ from S- note ranges. DR is calculated by dividing the average percent response to the S+ note range by the sum of the average total percent response to all note ranges. I excluded interrupted trials from the total before calculating proportion of response; this was calculated as: total # of responses divided by total number of trials less the # of interrupted trials, e.g., six responses to ten trials with three interrupted trials would result in an adjusted response rate of 6/7 (see Guillette et al., 2010, for additional details of the calculations).

All repeated measures ANOVAs were accompanied by a Mauchly's Test of Sphericity. If the assumption of sphericity was violated then Greenhouse-Geisser adjustments were made to the degrees of freedom used to determine the critical F-value.

Due to the large variation in the number of trials an individual chickadee took to reach training criterion, each bird's acquisition data was normalized using the Vincentization method

so that chickadees could be compared within and across conditions. Normalization allowed comparison between individuals, as one bird met learning criteria after eighteen blocks of trials while another met criteria after 54. Vincentizing was accomplished by dividing the total number of blocks a bird required to meet criterion by ten; this determined how many blocks of trials were averaged into a Vincentized block. The remainder of blocks were evenly parsed and averaged into the ten Vincentized blocks (e.g., if a bird had twenty-three blocks of data, each Vincentized block was an average of two blocks worth of trials and blocks 4,5, and 6 would have three blocks worth of trials).

Results & Discussion

Sex. Using a paired *t*-test, there was no significant difference between the number of bins to criteria between male ($M = 57.5$) and female ($M = 39.5$) chickadees ($t_{(7)} = 1.50, p = 0.176$). Additional statistical analyses were carried out comparing normalized proportion of responding between the S+ stimuli range (D4/D#4) and both S- stimulus ranges (C4/C#4 and E4/F4). Using a 2 (Sex) \times 3 (Note Range) repeated measures ANOVA, I found there was a significant effect main effect of note range ($F_{(2, 28)} = 436.919, p \leq 0.001$) and there was no significant effect of note range \times sex interaction ($F_{(2, 28)} = 0.837, p = 0.444$).

Discrimination Training

Results suggest that the chickadees ($n = 18$, 8 male and 8 female) learned the discrimination task before progressing to Generalization testing. I carried out pairwise planned comparisons, comparing normalized proportion of responding between the S+ stimuli range (D4/D#4) and both S- stimulus ranges (C4/C#4 and E4/F4) [Fig. 3.1]. Tests of significance were

corrected for family-wise error rates using Bonferroni correction ($\alpha = 0.025$). The mean proportion of response by chickadees to note ranges were: C4/C#4, $M = 0.197$; D4/D#4, $M = 0.829$; and E4/F4, $M = 0.12$. Chickadees had statistically significant differences in responding between the C4/C#4 - D4/D#4 ranges ($t_{(15)} = -22.417, p \leq 0.001$), and between the D4/D#4 - E4/F4 ranges ($t_{(15)} = 24.305, p \leq 0.001$).

Learning. Results suggest that there were no differences in discrimination learning rates for birds assigned to each Transfer testing ($n = 4$) experimental condition. I examined the DRs for each transfer condition to determine if there were differences in learning speed prior to Generalization testing and Transfer testing [Fig. 3.2]. Vincentized learning curves for Discrimination training were examined using an omnibus 4 (Condition) \times 10 (Block) repeated measures ANOVA and a significant main effect of block ($F_{(3,38)} = 51.420, p \leq 0.001$), and no significant interaction effect of block \times Condition ($F_{(9,38)} = 0.618, p = 0.785$).

Generalization Testing

Intra-octave Generalization testing. There was no evidence of generalization in the Intra-octave condition [Fig. 3.3]. The normalized proportion of responding was compared the D4/D#4 stimulus range and both of the C4/C#4 and E4/F4 note ranges, G#4/A4 stimulus range and both F#4/G4 and A#4/B4 note ranges. A one-way repeated measures ANOVA indicated a significant difference in responding across note ranges ($F_{(5, 35)} = 13.618, p = 0.001$). The omnibus repeated measures One-way ANOVA was followed by pairwise planned comparisons. Tests of

significance were corrected for family-wise error using the Bonferroni correction method ($\alpha = 0.013$). The mean proportion of response by chickadees to note ranges were: C4/C#4, $M = 0.225$, D4/D#4, $M = 0.796$; E4/F4, $M = 0.153$; F#4/G4, $M = 0.375$; G#4/A4, $M = 0.312$; and A#4/B4, $M = 0.51$. Pairwise comparisons revealed a significant difference in responding between: C4/C#4 - D4/D#4 ($t_{(7)} = -6.39, p \leq 0.001$), F#4/G4 - G#4/A4 ($t_{(7)} = 10.634, p \leq 0.001$), and no significant difference was observed between G#4/A4 - A#4/B4 ($t_{(7)} = 0.748, p = 0.479$), and between D4/D#4 - E4/F4 ($t_{(7)} = -2.08, p = 0.076$).

Inter-octave Generalization testing. There was no evidence of generalization in the Inter-octave condition as would have been expected by pitch chroma use [Fig. 3.4]. The normalized proportion of responding was compared the D4/D#4 stimulus range and both of the C4/C#4 and E4/F4 note ranges, C5/C5# stimulus range and both D5/D5# and E5/F5 note ranges. A repeated measures One-way ANOVA indicated a significant difference in response across note range ($F_{(2, 18)} = 11.845, p \leq 0.001$). Tests of significance were corrected for family-wise error using the Bonferroni correction method ($\alpha = 0.013$). The mean proportion of response by chickadees to note ranges were: C4/C#4, $M = 0.309$, D4/D#4, $M = 0.887$; E4/F4, $M = 0.184$; F#4/G4, $M = 0.343$; G#4/A4, $M = 0.291$; and A#4/B4, $M = 0.391$. Pairwise comparisons revealed a significant difference in responding between: C4/C#4 - D4/D#4 ($t_{(7)} = -25.690, p \leq 0.001$), F#4/G4 - G#4/A4 ($t_{(7)} = 24.642, p \leq 0.001$), and no significant difference was observed between G#4/A4 - A#4/B4 ($t_{(7)} = 0.398, p = 0.703$), and between D4/D#4 - E4/F4 ($t_{(7)} = -0.774, p = 0.464$).

Transfer Testing

Intra-octave Original-transfer Testing. There was no evidence of transfer in the Intra-octave Original-transfer condition as predicted by a transposition of the learned reinforcement contingencies [Fig. 3.5]. The normalized proportion of responding was compared the D4/D#4 stimulus range and both of the C4/C#4 and E4/F4 note ranges, G#4/A4 stimulus range and both F#4/G4 and A#4/B4 note ranges. An omnibus repeated measures ANOVA indicated a significant effect of response rates across note ranges ($F_{(5,15)} = 101.361, p \leq 0.001$). Planned comparisons were carried out on the first 960 trials of Transfer training. Tests of significance were corrected for family-wise error using the Bonferroni correction method ($\alpha = 0.013$). The mean proportion of response by chickadees to note ranges were: C4/C#4, $M = 0.187$, D4/D#4, $M = 0.887$; E4/F4, $M = 0.148$; F#4/G4, $M = 0.817$; G#4/A4, $M = 0.959$; and A#4/B4, $M = 0.151$. Pairwise comparisons revealed a significant difference in responding between: C4/C#4 - D4/D#4 ($t_{(3)} = -17.620, p \leq 0.001$), and D4/D#4 - E4/F4 ($t_{(3)} = 21.310, p \leq 0.001$); and no significant difference was observed between F#4/G4 - G#4/A4 ($t_{(7)} = -0.829, p = 0.468$), and between G#4/A4 - A#4/B4 ($t_{(7)} = -1.003, p = 0.390$).

Intra-octave Partial-reversal Transfer Testing. There was no evidence of transfer in the Intra-octave Partial-reversal condition as predicted by the use of an AFRS [Fig. 3.6]. The normalized proportion of responding was compared the D4/D#4 stimulus range and both of the C4/C#4 and E4/F4 note ranges, G#4/A4 stimulus range and both F#4/G4 and A#4/B4 note ranges. An omnibus repeated measures ANOVA indicated a significant effect of response rates across note ranges ($F_{(5,15)} = 9.363, p \leq 0.001$). Tests of significance were corrected for family-wise error

using the Bonferroni correction method ($\alpha = 0.013$). The mean proportion of response by chickadees to note ranges were: C4/C#4, $M = 0.162$, D4/D#4, $M = 0.726$; E4/F4, $M = 0.190$; F#4/G4, $M = 0.209$; G#4/A4, $M = 0.306$; and A#4/B4, $M = 0.567$. I found a significant effect of note range on response rates. Pairwise comparisons revealed a significant difference in responding between: C4/C#4 - D4/D#4 ($t_{(3)} = -5.955$, $p = 0.009$); no significant difference was observed between D4/D#4 - E4/F4 ($t_{(3)} = 4.528$, $p = 0.02$), F#4/G4 - G#4/A4 ($t_{(7)} = -1.858$, $p = 0.16$), and between G#4/A4 - A#4/B4 ($t_{(7)} = -1.681$, $p = 0.191$).

Inter-octave Original-transfer testing. There was no evidence of transfer in the Intra-octave Partial-reversal condition as predicted by the perception of pitch chroma [Fig. 3.7]. The normalized proportion of responding was compared the D4/D#4 stimulus range and both of the C4/C#4 and E4/F4 note ranges, C5/C#5 stimulus range and both D5/D#5 and E5/F5 note ranges. An omnibus repeated measures ANOVA indicated a significant effect of response rates across note ranges ($F_{(5, 15)} = 42.350$, $p \leq 0.001$). Tests of significance were corrected for family-wise error using the Bonferroni correction method ($\alpha = 0.013$). The mean proportion of response by chickadees to note ranges were: C4/C#4, $M = 0.237$, D4/D#4, $M = 0.838$; E4/F4, $M = 0.211$; C5/C#5, $M = 0.1323$; D5/D#5, $M = 0.145$; and E5/F5, $M = 0.932$. Pairwise comparisons revealed a significant difference in responding between: C4/C#4 - D4/D#4 ($t_{(3)} = -13.051$, $p = 0.001$), D4/D#4 - E4/F4 ($t_{(3)} = 15.286$, $p = 0.001$), and no significant difference was observed between C5/C#5 - D5/D#5 ($t_{(3)} = -0.204$, $p = 0.852$), and between D5/D#5 - E5/F5 ($t_{(3)} = 1.075$, $p = 0.361$).

Inter-octave Partial-Reversal Transfer testing. There was evidence of transfer in the Intra-octave Partial-reversal condition as predicted by the perception of pitch chroma [Fig. 3.8]. An omnibus repeated measures One-way ANOVA indicated no significant difference in response across note ranges ($F_{(5, 15)} = 1.358, p = 0.294$). The normalized proportion of responding was compared the D4/D#4 stimulus range and both of the C4/C#4 and E4/F4 note ranges, C5/C#5 stimulus range and both D5/D#5 and E5/F5 note ranges. Tests of significance were corrected for family-wise error using the Bonferroni correction method ($\alpha = 0.013$). The mean proportion of response by chickadees to note ranges were: C4/C#4, $M = 0.411$, D4/D#4, $M = 0.301$; E4/F4, $M = 0.296$; C5/C#5, $M = 0.390$; D5/D#5, $M = 0.301$; and E5/F5, $M = 0.249$. This pattern of responding suggests there was no observed transfer from previously trained stimuli and novel stimuli; additionally, the introduction of response contingencies interfered with the maintenance of discrimination of the C4/C#4, D4/D#4, and E4/F4 note ranges.

Interference effect of the Partial-reversal of Response Contingencies

Examination of Intra-octave [Fig. 3.3] and Inter-octave Generalization testing [Fig. 3.4] suggests that chickadees in both conditions failed to generalize learned response contingencies to novel note ranges. In both conditions, chickadees maintained the discrimination of the C4/C#4, D4/D#4, and E4/F4 note ranges as trained in Discrimination training and demonstrate clear discrimination from C5/C#5, D5/D#5, and E5/F5. Particularly of note is that the Intra-octave Original-transfer [Fig. 3.5] and Inter-octave Original-transfer [Fig. 3.7] conditions showed no difference in responding when compared to Generalization testing, and suggests that the introduction of response contingencies to the C5/C#5, D5/D#5, and E5/F5 note ranges did not interfere with the discrimination of the C4/C#4, D4/D#4, and E4/F4 note ranges. Most

importantly, the chickadees in the Inter-octave Partial-reversal condition failed to discriminate any note ranges [Fig. 3.8]. This indicates that the partial-reversal of response contingencies in the Inter-octave Partial-reversal condition significantly interfered with the discrimination of the C4/C#4, D4/D#4, and E4/F4 note ranges, and suggests that chickadees perceived the C5/C#5, D5/D#5, and E5/F5 note ranges as perceptually similar. This strongly suggests the chickadees perceive pitch chroma.

Transfer Discrimination training

Intra-octave Original-transfer Discrimination training. Response patterns suggest that chickadees did learn the novel discrimination. The proportion of responding to each note range was examined to determine if the Intra-octave Original-transfer group were able to discriminate note ranges according to response contingencies. *t*-tests comparing normalized proportion of responding between the G#4/A4 note range and both F#4/G4 and A#4/B4 note ranges. Tests of significance were corrected for family-wise error rates using Bonferroni correction ($\alpha = 0.025$). The mean proportion of response by chickadees to note ranges were: F#4/G4, $M = 0.574$; G#4/A4, $M = 0.910$; and A#4/B4, $M = 0.379$. Chickadees had statistically significant differences in responding between the F#4/G4 - G#4/A4 ranges ($t_{(3)} = -5.132$, $p = 0.014$), and between the G#4/A4 - A#4/B4 ranges ($t_{(3)} = 5.514$, $p = 0.012$) [Fig. 3.9].

Intra-octave Partial-Reversal Transfer Discrimination training. Response patterns suggest that chickadees didn't learn the novel discrimination. The proportion of responding to each note

range was examined to determine if the Intra-octave Partial-Reversal group were able to discriminate note ranges according to response contingencies [Fig. 3.10]. *t*-tests comparing normalized proportion of responding between the G#4/A4 note range and both F#4/G4 and A#4/B4 note ranges. Tests of significance were corrected for family-wise error rates using Bonferroni correction ($\alpha = 0.025$). The mean proportion of response by chickadees to note rangers were: F#4/G4, $M = 0.261$; G#4/A4, $M = 0.232$; and A#4/B4, $M = 0.734$. Chickadees had no statistically significant difference in responding between the F#4/G4 - G#4/A4 ranges ($t_{(3)} = 0.995$, $p = 0.393$), and the G#4/A4 - A#4/B4 ranges ($t_{(3)} = -2.895$, $p = 0.063$).

Inter-octave Original-transfer Discrimination training. Response patterns suggest that chickadees did learn the novel discrimination. The proportion of responding to each note range was examined to determine if the Inter-octave Original-transfer group were able to discriminate note ranges according to response contingencies [Fig. 3.11]. *t*-tests comparing normalized proportion of responding between the S+ stimuli range (D5/D#5) and both S- stimulus ranges (C5/C#5 and E5/F5) [Fig. 3.11]. Tests of significance were corrected for family-wise error rates using Bonferroni correction ($\alpha = 0.025$). The mean proportion of response by chickadees to note rangers were: C5/C#5, $M = 0.199$; D5/D#5, $M = 0.941$; and E5/F5, $M = 0.302$. Chickadees had statistically significant differences in responding between the C5/C#5 – D5/D#5 ranges ($t_{(3)} = -10.910$, $p = 0.002$), and between the D5/D#5 – E5/F5 ranges ($t_{(3)} = 9.177$, $p = 0.003$).

Inter-octave Partial-reversal Transfer Discrimination training. Response patterns suggest that chickadees didn't learn the novel discrimination. The proportion of responding to each note range was examined to determine if the Inter-octave Partial-reversal group were able to discriminate note ranges according to response contingencies [Fig. 3.12]. *t*-tests comparing normalized proportion of responding between the S+ stimuli range (D5/D#5) and both S- stimulus ranges (C5/C#5 and E5/F5). Tests of significance were corrected for family-wise error rates using Bonferroni correction ($\alpha = 0.025$). The mean proportion of response by chickadees to note rangers were: C5/C#5, $M = 0.919$; D5/D#5, $M = 0.283$; and E5/F5, $M = 0.592$. Chickadees had statistically significant differences in responding between the C5/C#5 – D5/D#5 ranges ($t_{(3)} = 7.083$, $p = 0.006$), but not between the D5/D#5 – E5/F5 ranges ($t_{(3)} = -1.786$, $p = 0.172$) [Fig. 3.12].

Savings

As a secondary measure of learning, I examined savings between conditions as a measure of pattern generalization.

Initial proportion of response. I examined the initial proportion of response for the first 480 trials for each transfer condition. I found the proportion of response by each group was not significantly above chance (0.5): Intra-octave Original-transfer 95% CI [0.374, 0.621]; Intra-octave Partial-reversal transfer 95% CI [0.429, 0.686]; Inter-octave Original-transfer 95% CI [0.340, 0.980]; and Inter-octave Partial-reversal transfer 95% CI [0.471, 0.590].

Final proportion of response. I examined the final proportion of response for the Vincentized block of trials for each transfer condition. Using a one-way ANOVA, I found no statistically significant differences in the proportion of response by each group ($F_{(3,12)} = 1.498, p = 0.265$).

Transfer training learning curves. I examined the DRs for each transfer condition to determine if there were differences in learning speed during Transfer Discrimination training and found no group differences [Fig. 3.13]. Vincentized learning curves for Discrimination training were examined using an omnibus 4 (Condition) \times 10 (Block) repeated measures ANOVA and I found a significant effect of block on DR ($F_{(2, 27)} = 12.004, p \leq 0.001$). I found no significant interaction effect of block * treatment condition ($F_{(6,27)} = 1.613, p = 0.174$) on Vincentized learning curves, I compared the rate of learning between treatment conditions. Results suggest that there is no difference in learning between conditions during Transfer Discrimination training.

Savings and Learning Curves

Ostensibly, if chickadees do perceive pitch chroma as perceptual categories, it was expected that when trained in octave 4 and presented with novel frequencies from octave 5, note with similar pitch chroma would be treated similarly. Additionally, if presented with novel frequencies from octave 5 with response contingencies that are complimentary to octave 4 (e.g., Inter-octave Original-transfer) that there would be savings effects, while response contingencies that are opposed to those from training would impede learning. Therefore, I examined three measures of savings: initial DRs, final DRs, and learning curves. Initial DRs by chickadees

above chance levels would indicate a transfer of learned response contingencies; however, no conditions were observed to discriminate at higher than chance levels. Final DRs by chickadees did not vary between conditions, suggesting each group was treating the novel task as a novel discrimination. The final measure of savings was to examine the Vincentized learning curves of each condition; I observed no significant effect of block * treatment condition [Fig. 3.13]. Taken all together, although chickadees did learn the novel discrimination task, they did significantly differ in rates of learning.

Alternating pattern generalization

One of the main goals of this experiment was to verify the interpretation of results by Hoeschele et al. (2012) in a similar experiment. Hoeschele et al. (2012) had previously suggested that chickadees may have learned to generalize from using an AFRS. If chickadees are relying on an AFRS it would be expected that the learning of Intra-octave Partial-reversal Transfer testing response contingencies would be more rapid than Intra-octave Original-transfer testing. I observed no difference in the rates of learning between these two conditions [Fig. 3.13]. Additionally, neither the Intra-octave Original-transfer [Fig. 3.5] nor the Intra-octave Partial-reversal conditions [Fig. 3.6] showed any transfer in Transfer testing. Finally, in Transfer discrimination training, the Intra-octave Original-transfer group learned to discriminate the novel frequency ranges [Fig. 3.9] but the Intra-octave Partial-reversal group failed to learn this discrimination [Fig. 3.10]. Together, these observed results suggest that chickadees did not perceive the complimentary and reversed response contingencies differently, and this does not support the interpretation that chickadees in this experiment learned to generalize based on an alternating frequency range strategy.

Pitch Height Reliance over Pitch Chroma

My results provide conflicting evidence for whether black-capped chickadees perceive pitch chroma. Measures of savings and learning suggest there was no advantage for the Inter-octave Original-transfer condition in learning the novel discrimination task in Transfer Discrimination Training [Fig. 3.13]. This would be expected if the chickadees perceived pitch chroma related notes as being a perceptual category. However, the results from Transfer testing are in agreement with predictions for the partial reversal of response contingencies; where the Inter-octave Partial-reversal group is unable to maintain discrimination of the six trained notes [Fig. 3.8]. This would suggest that the chickadees do perceive pitch chroma but overall show a preference or reliance on pitch height perception; which resulted in no observed savings effects. That is, that the chickadees treated the Transfer Discrimination training task as a pitch height task and therefore a novel task.

Tables & Figures

Table 3.1 Group assignment Table

Non-differentiation training	All birds (n =16)			
Discrimination training				
Pre-testing				
Generalization testing	Intra-octave (n =8)		Inter-octave (n =8)	
Transfer testing & Transfer Discrimination training	Original-transfer (n =4)	Partial-reversal (n =4)	Original-transfer (n =4)	Partial-reversal (n =4)

Table 3.1. Group assignment Table. The table describes the division of birds into experimental conditions during the Discrimination training, Generalization testing, Transfer testing, and Transfer Discrimination training phases of the experiment. For Generalization testing birds were assigned to either Intra-octave or Inter-octave conditions. For Transfer testing birds were further divided into either Original-transfer or Partial-reversal conditions. Group assignment was unchanged for Transfer Discrimination training.

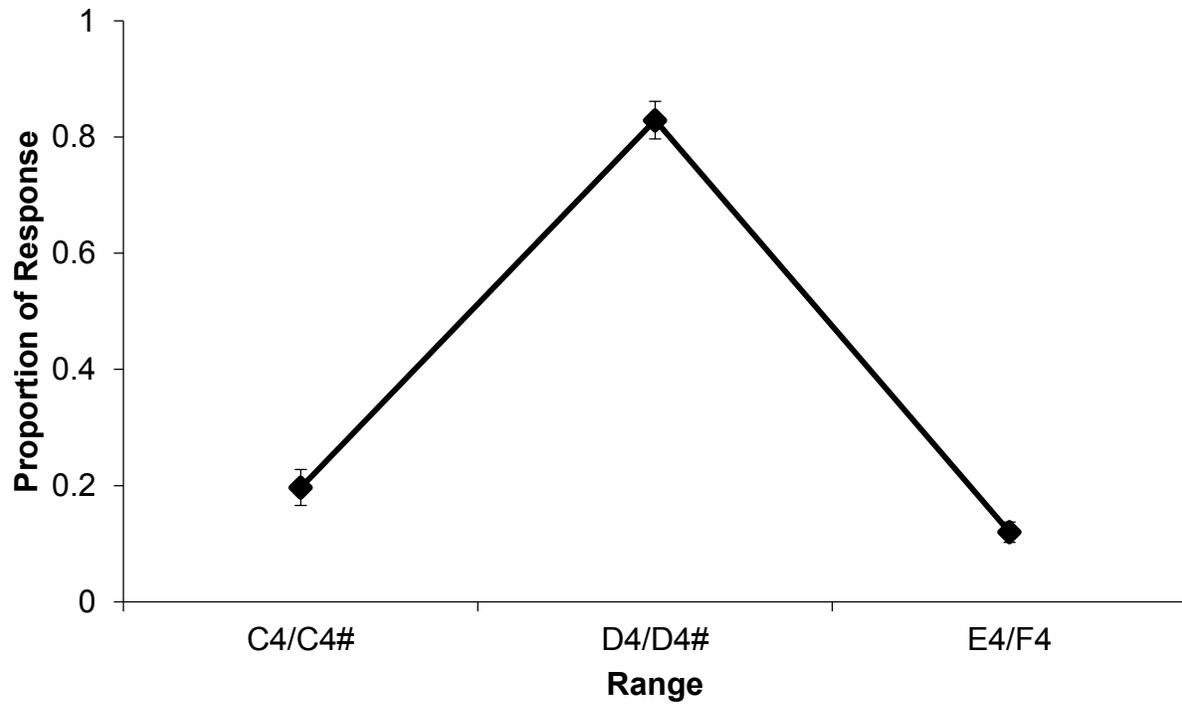
Figure 3.1. Discrimination training

Figure 3.1. Discrimination training. Graph depicts the normalized average proportion of responding during Discrimination training for black-capped chickadees. S+ stimuli range D4/D#4 and S- stimulus ranges C4/C#4 and E4/F4. Solid line indicates the average group response for participants. Error bars are \pm S.E.M.

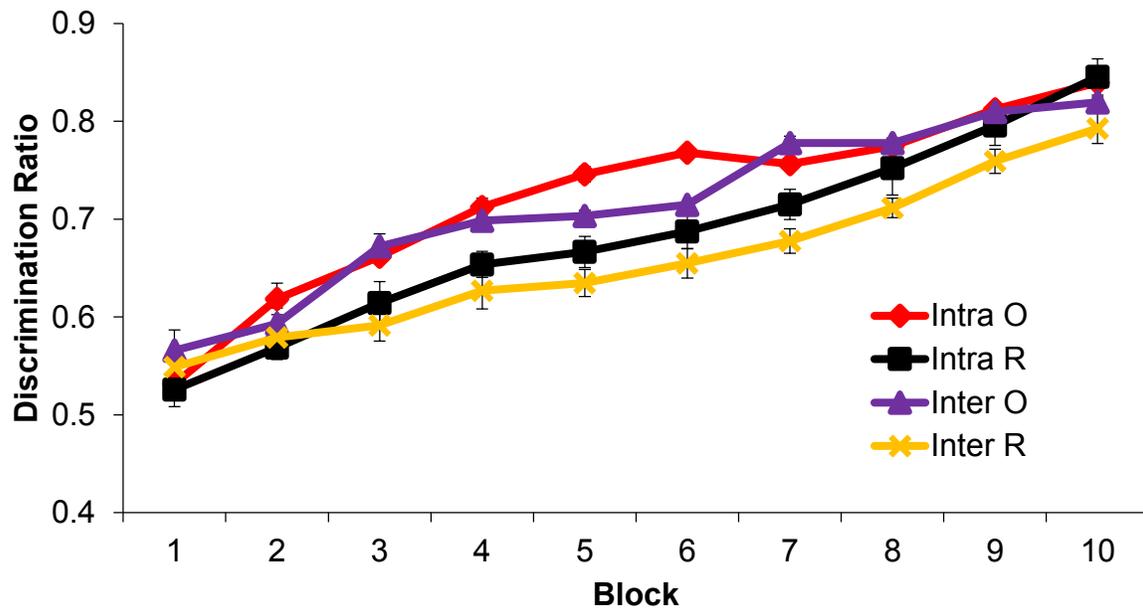
Figure 3.2. Discrimination training – Vincentized Learning Curve

Figure 3.2. Discrimination training Vincentized learning curves. Graph depicts the normalized learning curves during Discrimination training for black-capped chickadees. Error bars are \pm S.E.M.

Figure 3.3. Intra-octave Generalization testing

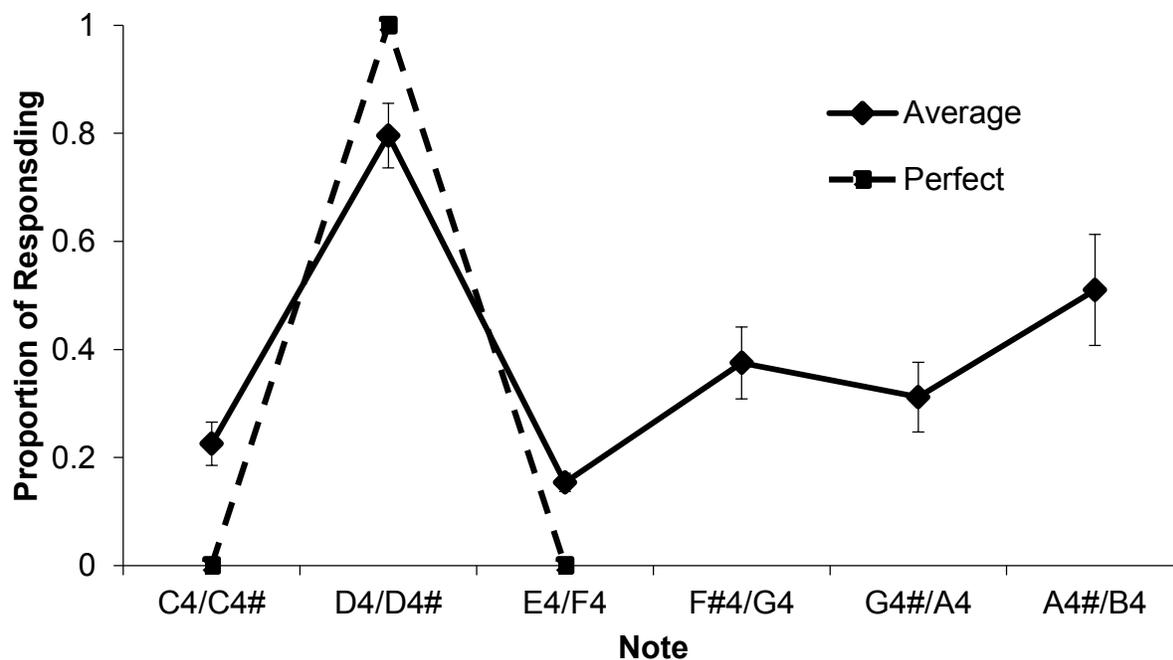


Figure 3.3. Intra-octave Generalization testing. Graph depicts the normalized average proportion of responding during Generalization testing for chickadees using six note pairs from the 4th octave. Solid line indicates the average group response for participants. Dashed line indicates the expected response if chickadees responded based on response contingencies. S+ stimuli range D4/D#4 and S- stimulus ranges C4/C#4 and E4/F4. Error bars are \pm S.E.M.

Figure 3.4. Inter-octave Generalization testing

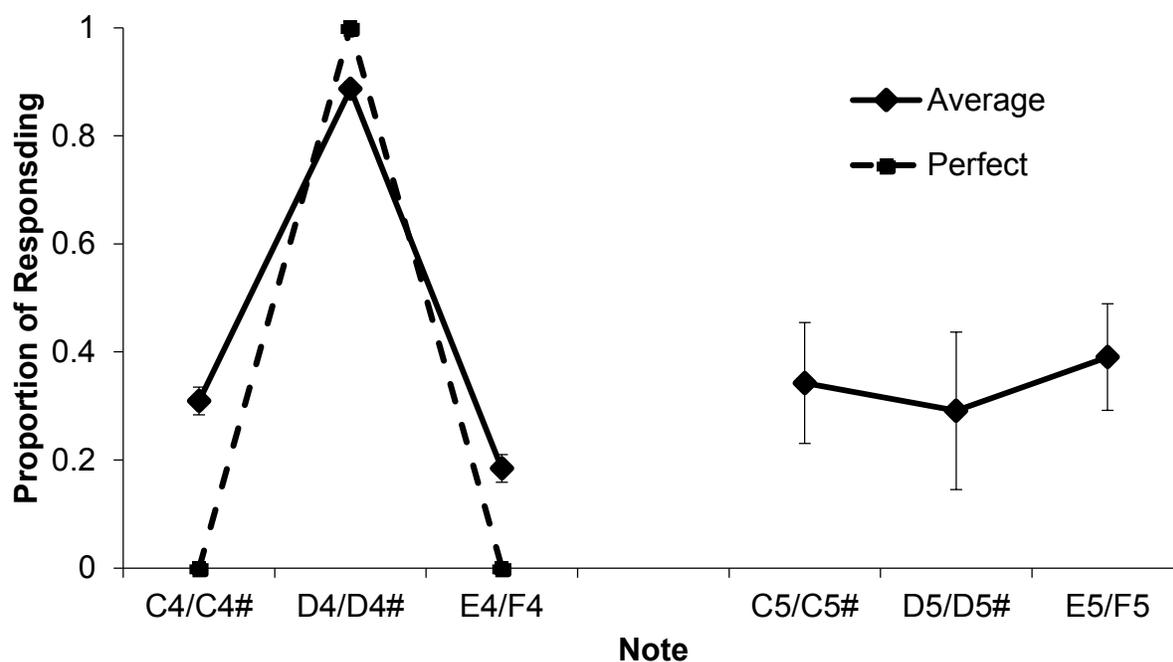


Figure 3.4. Inter-octave Generalization testing. Graph depicts the normalized average proportion of responding during Generalization testing for chickadees using three note pairs from the 4th octave and three note pairs from the 5th octave. Solid line indicates the average group response for participants. Dashed line indicates the expected response if chickadees responded based on response contingencies. S+ stimuli range D4/D#4 and S- stimulus ranges C4/C#4 and E4/F4. Error bars are \pm S.E.M.

Figure 3.5. Intra-octave Original-transfer testing

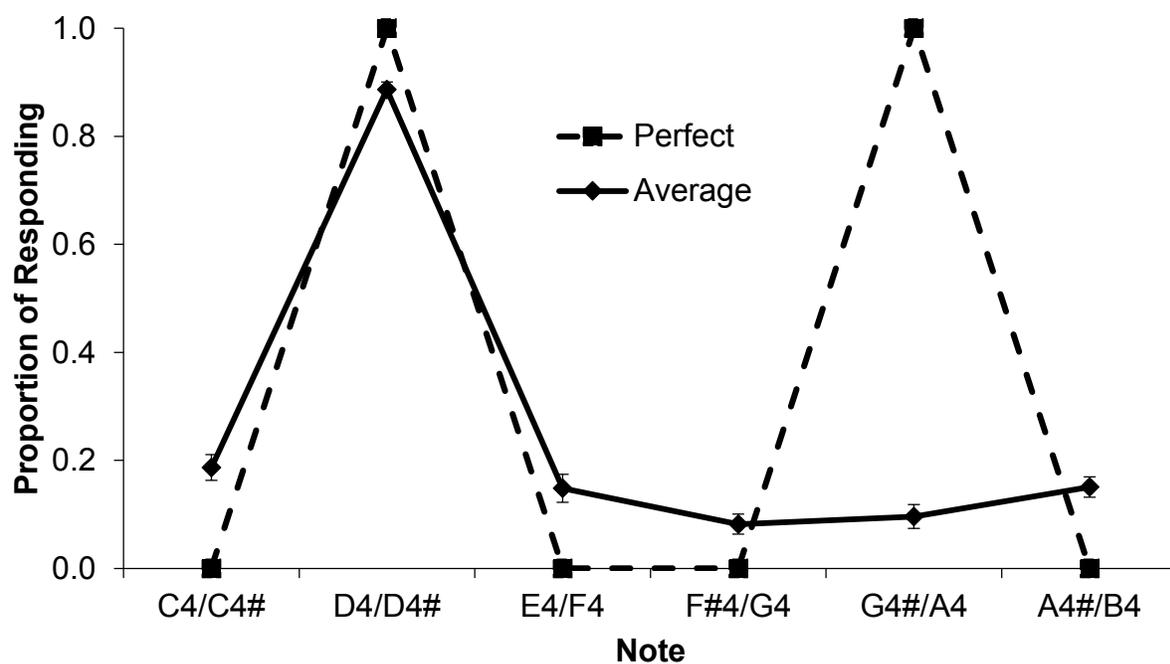


Figure 3.5. Intra-octave Original-transfer testing. Participants normalized average proportion of responding during Transfer testing for Intra-octave Original-transfer condition chickadees using six note pairs from the 4th octave. S+ ranges: D4/D#4 and G#4/A4. S- Ranges: C4/C#4, E4/F4, F#4/G4, and A#4/B4. Solid line indicates the average group response. Dashed line indicates expected responding based on perfect discrimination. Error bars are \pm S.E.M.

Figure 3.6. Intra-octave Partial-reversal Transfer testing

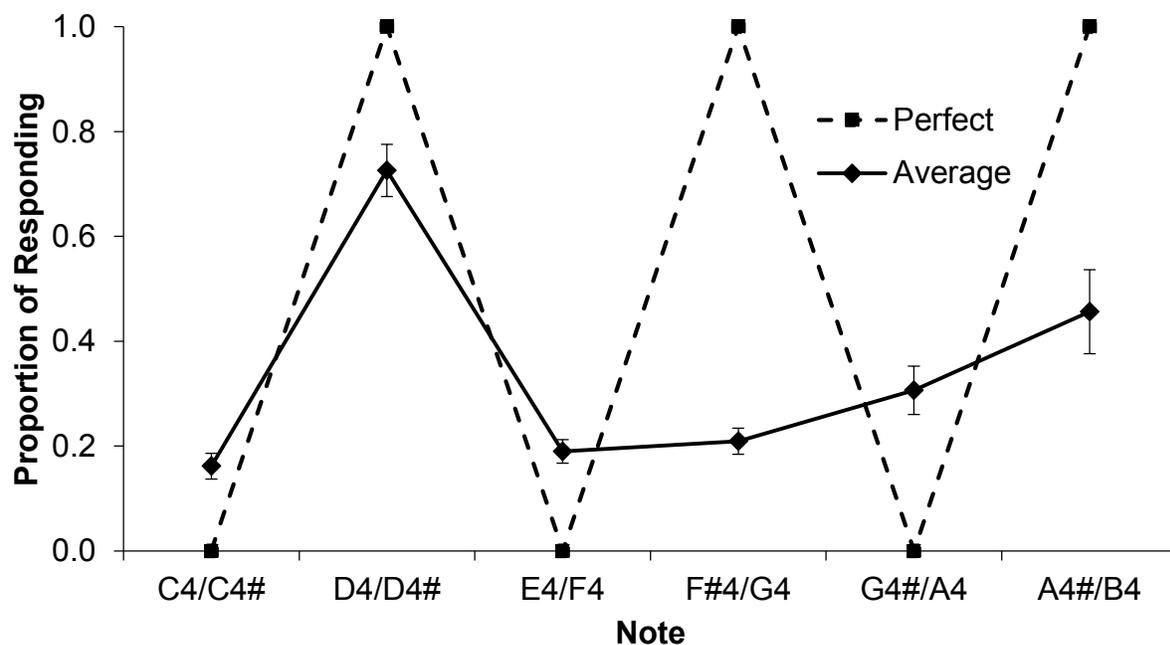


Figure 3.6. Intra-octave Partial-reversal Transfer testing. Participants normalized average proportion of responding during Transfer testing for Intra-octave Partial-reversal condition chickadees using six note pairs from the 4th octave. S+ ranges: D4/D#4, F#4/G4, and A#4/B4. S- Ranges: C4/C#4, E4/F4, and G#4/A4. Dashed line indicates expected responding based on perfect discrimination. Solid line indicates the average group response. Error bars are \pm S.E.M.

Figure 3.7. Inter-octave Original-transfer testing

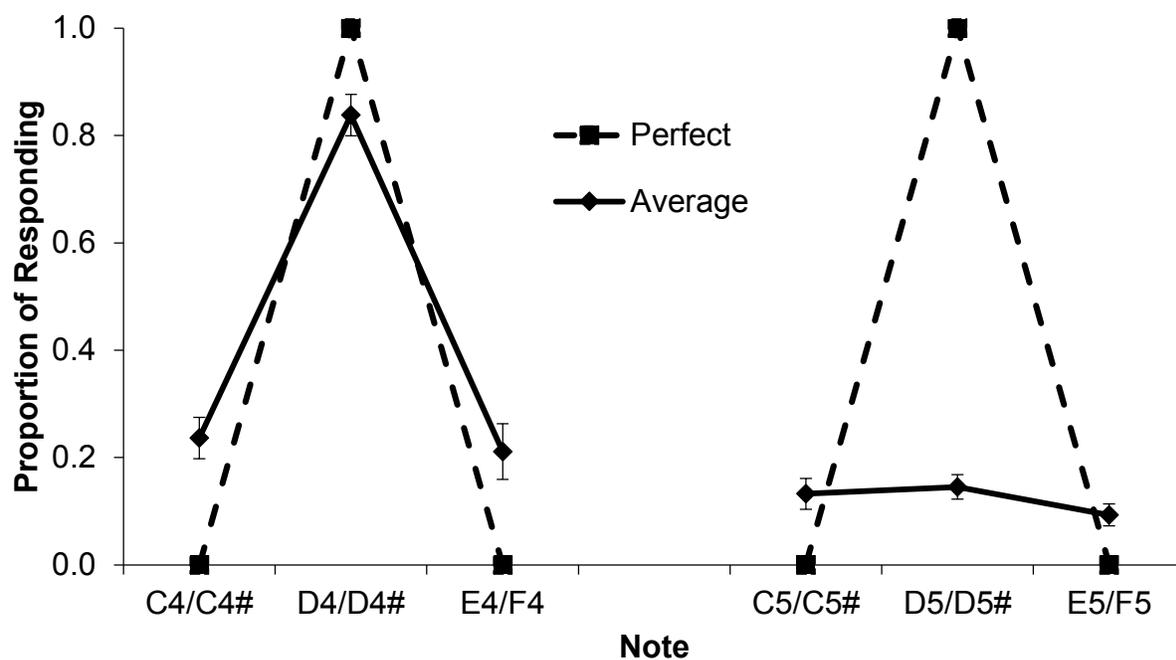


Figure 3.7. Inter-octave Original-transfer testing. Participants normalized average proportion of responding during Transfer testing for Inter-octave Original-transfer condition chickadees using three note pairs from the 4th octave and three note pairs from the 5th octave. S+ ranges: D4/D#4 and D5/D#5. S- ranges: C4/C#4, E4/F4, C5/C#5, and E5/F5. Dashed line indicates expected responding based on perfect discrimination. Solid line indicates the average group response. Error bars are \pm S.E.M.

Figure 3.8. Inter-octave Partial-reversal Transfer testing

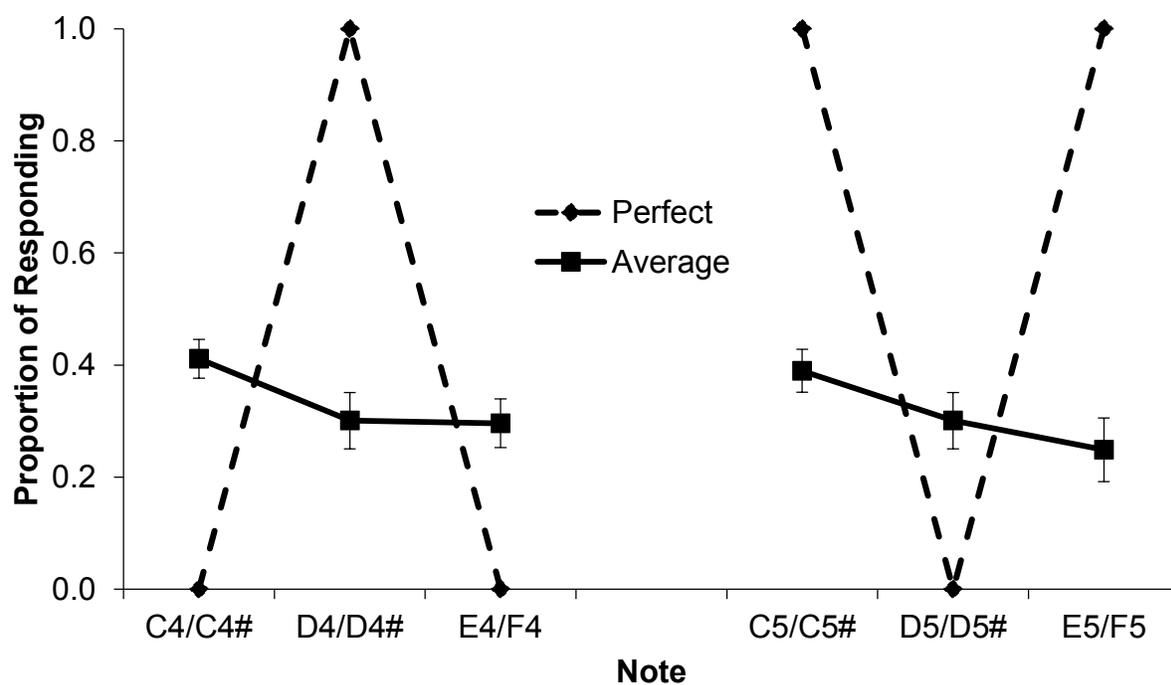


Figure 3.8. Inter-octave Partial-reversal Transfer testing. Participants normalized average proportion of responding during Transfer testing for Inter-octave Partial-reversal Transfer condition chickadees using three note pairs from the 4th octave and three note pairs from the 5th octave. S+ ranges: D4/D#4, C5/C#5, and E5/F5. S- ranges: C4/C#4, E4/F4, and D5/D#5. Dashed line indicates expected responding based on perfect discrimination. Solid line indicates the average group response. Error bars are \pm S.E.M.

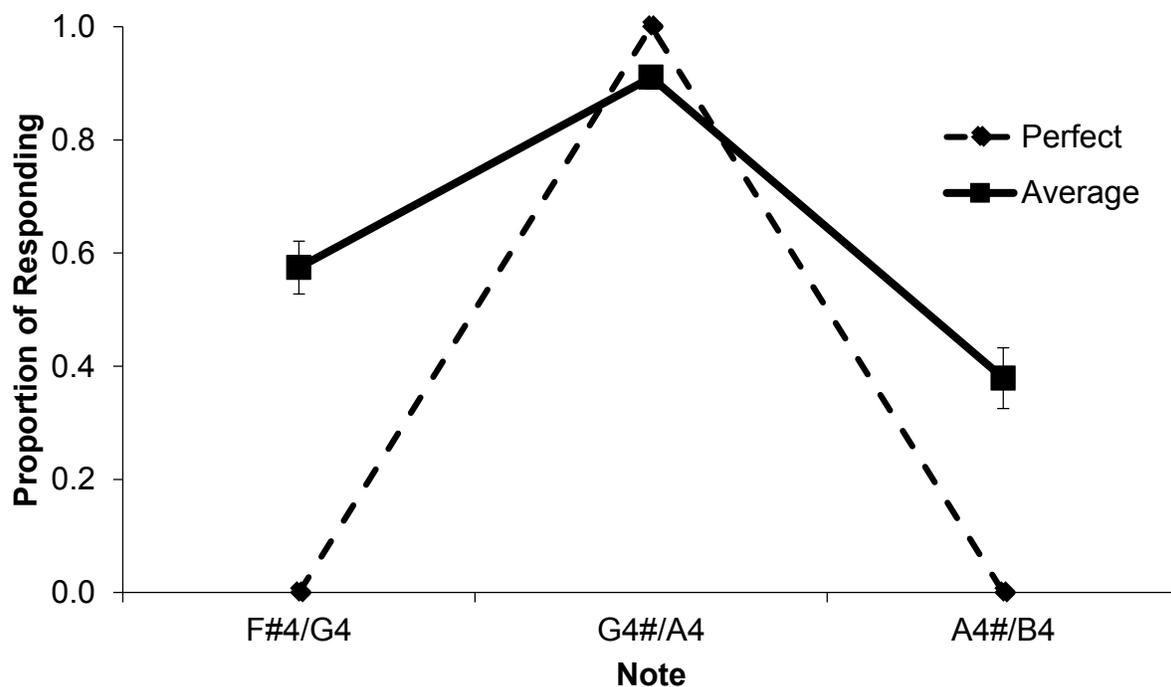
Figure 3.9. Intra-octave Original-transfer Discrimination training

Figure 3.9. Intra-octave Original-transfer Discrimination training. Participants normalized average proportion of responding during Transfer Discrimination training for Intra-octave original-transfer condition chickadees using three note pairs from the 4th octave. S+ ranges: G#4/A4. S- Ranges: F#4/G4, and A#4/B4. Solid line indicates the average group response. Dashed line indicates expected responding based on perfect discrimination. Error bars are \pm S.E.M.

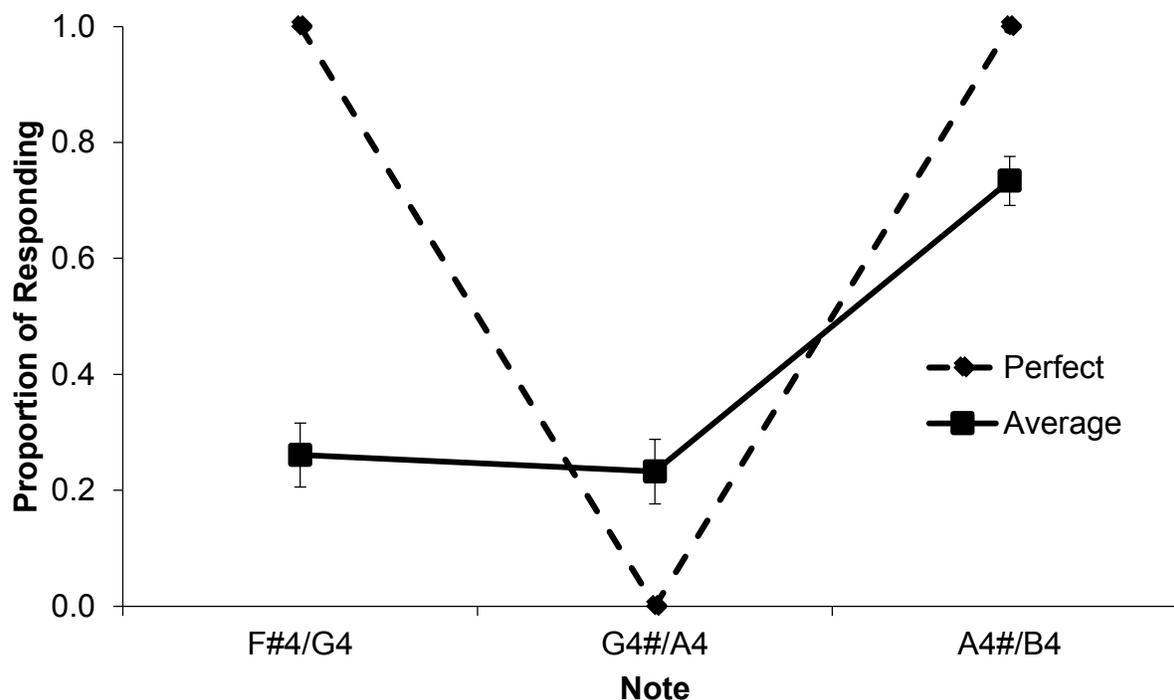
Figure 3.10. Intra-octave Partial-reversal Discrimination training

Figure 3.10. Intra-octave Partial-reversal Transfer Discrimination training. Participants normalized average proportion of responding during Transfer Discrimination training for Intra-octave original-transfer chickadees using three note pairs from the 4th octave. S+ Ranges: F#4/G4, and A#4/B4. S- ranges: G#4/A4. Solid line indicates the average group response. Dashed line indicates expected responding based on perfect discrimination. Error bars are \pm S.E.M.

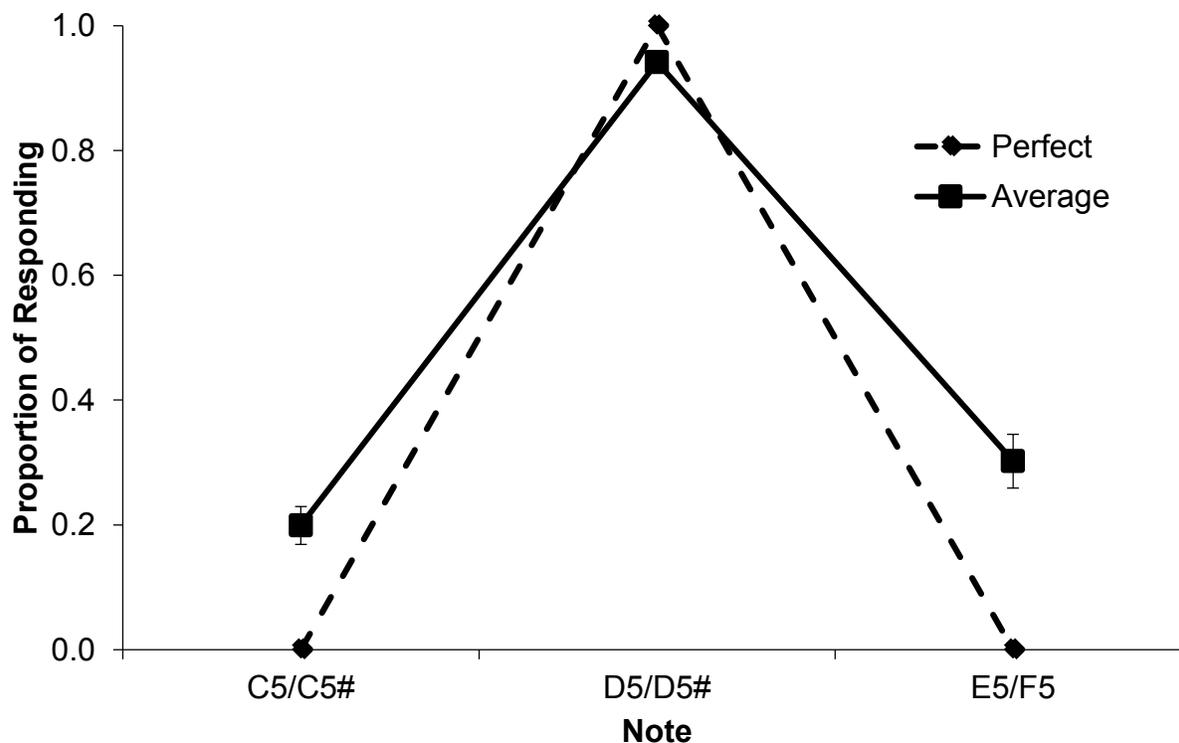
Figure 3.11. Inter-octave Original-transfer Discrimination training

Figure 3.11. Inter-octave Original-transfer Discrimination training. Participants normalized average proportion of responding during Transfer Discrimination training for Inter-octave original-transfer chickadees using three note pairs from the 5th octave. S+ ranges: D5/D#5. S- ranges: C5/C#5, and E5/F5. Dashed line indicates expected responding based on perfect discrimination. Solid line indicates the average group response. Error bars are \pm S.E.M.

Figure 3.12. Inter-octave Partial-reversal Discrimination training

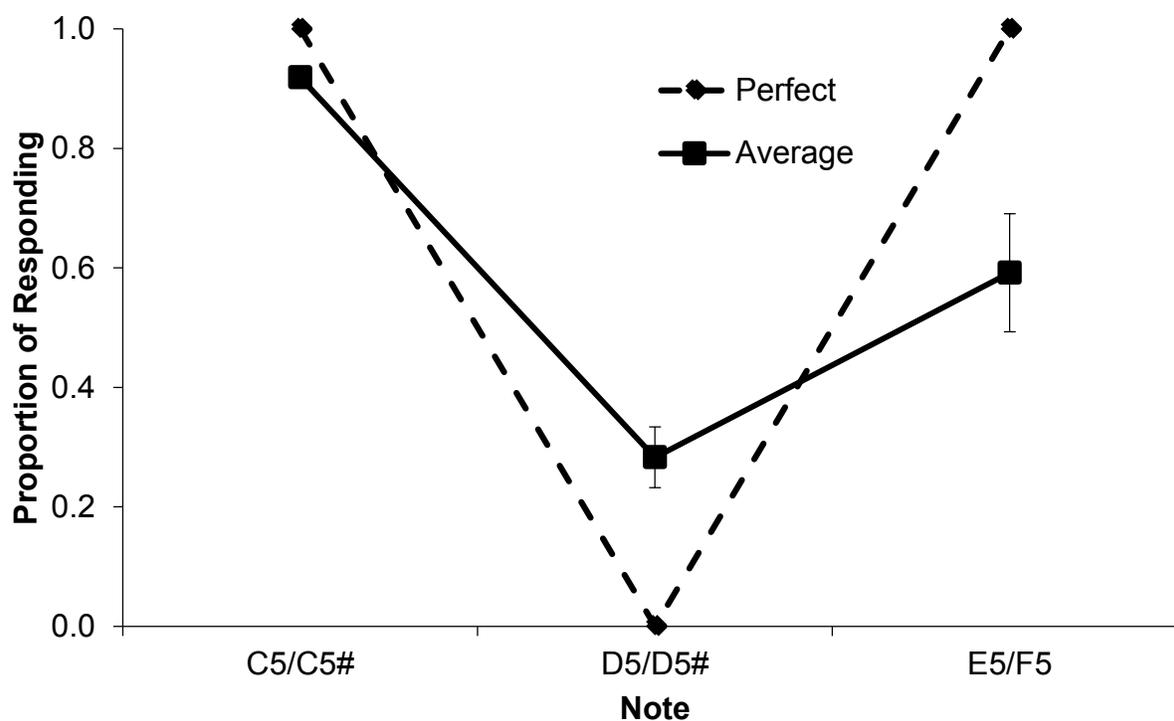


Figure 3.12. Inter-octave Partial-reversal Transfer Discrimination training. Participants normalized average proportion of responding during Transfer Discrimination training for Inter-octave Partial-reversal Transfer chickadees using three note pairs from the 5th octave. S+ ranges: D4/D#4, C5/C#5, and E5/F5. S- ranges: C4/C#4, E4/F4, and D5/D#5. Dashed line indicates expected responding based on perfect discrimination. Solid line indicates the average group response. Error bars are \pm S.E.M.

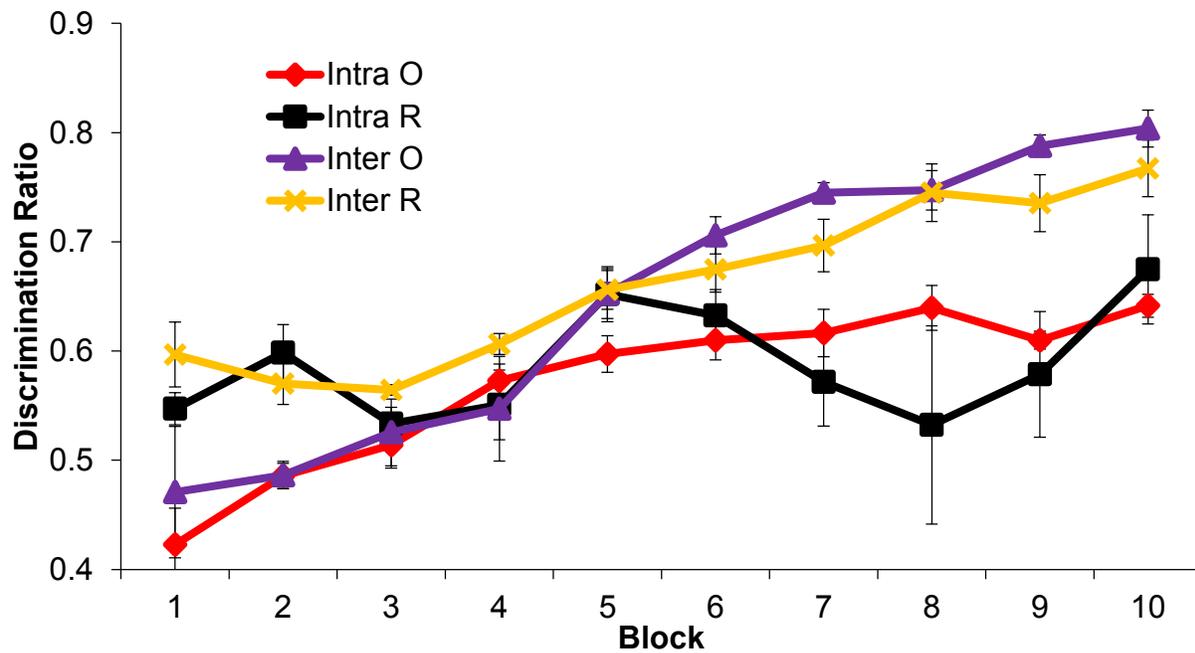
Figure 3.13. Transfer Discrimination training - Vincentized Learning Curves

Figure 3.13. Discrimination training Vincentized learning curves. Graph depicts the normalized learning curves during Transfer Discrimination training for black-capped chickadees. Error bars are \pm S.E.M.

General Discussion

The goal of this series of experiments was to determine if chickadees perceive pitch chroma; previous studies were inconclusive regarding pitch chroma perception in chickadees (Hoeschele et al., 2013). The first experiment used human participants as a positive control for a modified procedure from Hoeschele et al. (2013). The positive control served to confirm that my procedure could detect octave equivalence, that is, that modifications to the experimental procedure didn't significantly affect the detection of pitch chroma perception. I found that the modifications lead to no generalization based on pitch height or pitch chroma; this was in contrast to results of Hoeschele et al. (2013) where their procedure did result in pitch chroma generalization. However, pitch chroma perception was still detected in the Transfer testing phase. The second experiment tested an analogous procedure with black-capped chickadees. I found that chickadees didn't generalize based on pitch height or pitch chroma, but I found evidence for pitch chroma perception in chickadees in the Transfer testing phase, similar to the results with humans.

Comparison of Pitch Use Across Species

The primary motivation of this work was to examine and establish any similarities in perception of pitch height and pitch chroma between chickadees and humans. To accomplish this, I compared the results obtained from Discrimination training, Generalization testing, and Transfer testing. The methodologies for both experiments, human and chickadee, were kept as similar as possible to allow for the most direct comparison between species; any procedural differences primarily stem from the ability to keep animal subjects in the experiments for long

periods of time and the inability to do so with human participants. The second major difference is experiential: the ability to control the exposure to stimuli used in experiment is many times greater with chickadees than human participants. Humans are exposed to the Western musical scale (the musical scale from which the experimental stimuli were selected) in everyday life, and this likely impacts how the participants perceive the underlying relationships between experimental stimuli.

To compare chickadees and humans in the octave equivalence task, it is first necessary to establish that both species learned the task to a similar level. Chickadees were required to learn the discrimination task to criterion ($DR \geq 0.80$), while human participants were selected based on performance criteria. Analysis for both species indicates that both species learned to discriminate the three two note ranges in Discrimination training [Fig. 4.1]. There was higher overall responding by human participants, but this may be the consequence of two factors: the amount of time each species was trained and the human data included all trials whereas chickadee data only included the final block of trials at criteria. While considering these two differences, results suggest both species had learned to discriminate the note ranges to a highly proficient level.

Neither species generalized the learned discrimination to the Intra-octave [Fig. 4.2] nor the Inter-octave note ranges [Fig. 4.3]. There was a key difference in the response patterns of both species; chickadees maintained the discrimination of C4/C#4, D4/D#4, and E4/F4, but the human participants failed to maintain this discrimination. These results suggest that the chickadees discriminated by the identity of the note based on pitch height rather than pitch chroma or using the alternating frequency range strategy. The human participants may have been responding according to a general rule based on relative pitch. The human Intra-octave data suggests that the learned discrimination was applied to the whole range of twelve notes instead

of the six training notes. This species difference is understandable as chickadees excel at pitch height perception when compared with human participants (Weisman et al., 2010). Results suggest that both species learned the discrimination based on a pitch height characteristics. Additionally, the results suggest that neither species attended to pitch chroma during the discrimination task or the generalization test.

These experiments were designed to determine if chickadees perceived pitch chroma, because previous negative results may have been due to not differentiating pitch height and pitch chroma use. Generalization results suggest that neither chickadees nor human participants attended to pitch chroma, but this does not necessarily mean that neither group perceives pitch chroma. The Intra-octave Original-transfer was used to test if either species could transfer the learned response contingencies based on pitch height. There was a possibility that chickadees were transposing the learned response contingencies to all novel note ranges; the successful transfer in the Intra-octave Original-transfer condition and Inter-octave Original-transfer condition would have supported this interpretation. Neither species demonstrated transfer in Intra-octave Original-transfer [Fig. 4.4], suggesting that transposition of the learned response contingencies was not occurring. The Intra-octave Partial-reversal condition was used to examine if either species was applying alternating frequency range pattern; there was no evidence for the use of this strategy in either humans or chickadees [Fig. 4.5]. The Inter-octave Original-transfer condition was used to test if either species could transfer on the basis of pitch chroma; I found that humans did transfer but chickadees did not [Fig. 4.6]. The Inter-octave Partial-reversal condition was used as a secondary test of pitch chroma perception and was based on the assumption that pitch chroma matched notes should be perceived as being similar. The partially reversed response contingencies resulted in human participants failing to maintain a well-trained

discrimination [Fig. 4.7]. The most interesting finding was that chickadees demonstrated a similar loss in discrimination to humans [Fig. 4.7], even though chickadees failed to demonstrate pitch chroma use in the Inter-octave Original-transfer task. Taken together, there is strong evidence to suggest that both humans and chickadees perceived pitch chroma, but in this task chickadees relied on pitch height perception rather than pitch chroma to learn the trained discriminations.

A possible alternate explanation is that the note range used for the Intra-octave condition was too similar to the note ranges used in Discrimination training, and resulted in a more difficult discrimination than the Inter-octave condition. Future experiments could use octave 5 notes for the Intra-octave condition (F#5/G5, G#5/A5, and A#5/B5), thereby changing the proximity of the note ranges. Additionally, it is possible that chickadees prefer to discriminate based on pitch height due to their superior AP abilities; to test this, a task would need to require chickadees to selectively discriminate based on pitch chroma to demonstrate stronger evidence for pitch chroma perception.

Implications and Future Directions

My findings further support a position held by Hoeschele et al. (2013), that pitch perception is not a unitary ability but consists of a number of component perceptual abilities: absolute pitch, relative pitch, pitch height, and pitch chroma perception. Each of these abilities is active in parallel with each other ability during auditory processing, and must be accounted for when designing an experiment and interpreting experimental results.

The finding that chickadees perceive pitch chroma supports Darwin's "Musical protolanguage" theory. As discussed in Chapter 1, "Musical protolanguage" posits that there must be near-universal perception of musicality and musical qualities included under the

umbrella of musicality, such as pitch chroma and octave equivalence. My findings add to the evidence supporting the notion of a “Musical protolanguage”, and suggest that when searching for universal musicality researchers must account for the etiological constraints within each species (e.g., preferential use of pitch height and the frequency range constraint in songbirds). Although my findings add to the growing evidence for a “Musical protolanguage”, the phylogenetic distance between songbirds and the hominid lineage must be acknowledged. My findings suggest that chickadees perceive pitch chroma and this ability may have existed in a common ancestor, but this does not mean that pitch chroma perception was a component of the “Musical protolanguage”. To date, there has been no evidence to suggest that chickadees use octave equivalence in their communication system.

Future experiments should focus on establishing pitch chroma perception in other songbird species, particularly species with complex vocal repertoires, such as starlings or zebra finches. An experiment by Cynx (1995), found negative results for pitch chroma based generalization in zebra finches and starlings; however, Cynx concluded that the negative finding was due to a frequency range constraint caused by the novelty of the testing frequencies. In my experiment, I introduced all frequencies in Non-differentiation training to mitigate the effects of both neophobia and the frequency range constraint. It would be valuable to re-examine pitch chroma perception in these two species while accounting for both the frequency range constraint and the preferential use of pitch height. Establishing pitch chroma perception in other species would suggest pitch chroma perception is a conserved perceptual ability, and suggest a significant role in evolution of the proposed “Musical protolanguage”; this is especially important if there is no usage of octave equivalence in songbird communication. Second, future research should focus on identifying the role of octave equivalence in songbird communication.

If pitch chroma perception is a musical universal involved in the evolution of a “Musical protolanguage”, it should play a role in communication.

Conclusion

The findings of Hoeschele et al. (2013), suggest that black-capped chickadees do not perceive pitch chroma; I propose a reinterpretation consistent with their findings, that black-capped chickadees do perceive pitch chroma but highly favour the use of pitch height and because of this they failed to demonstrate the use of pitch chroma in Hoeschele et al. (2013). Experiments 1 and 2 suggest that the preferential use of pitch height over pitch chroma perception may be etiologically bound, and requires experimental finagling to indirectly assess the perceptual ability of the subject. Having established pitch chroma perception in chickadees, we are now ready to ask: Do chickadees use octave equivalence perception in communication? These findings further the possibility songbirds are a viable model for the study of human language learning.

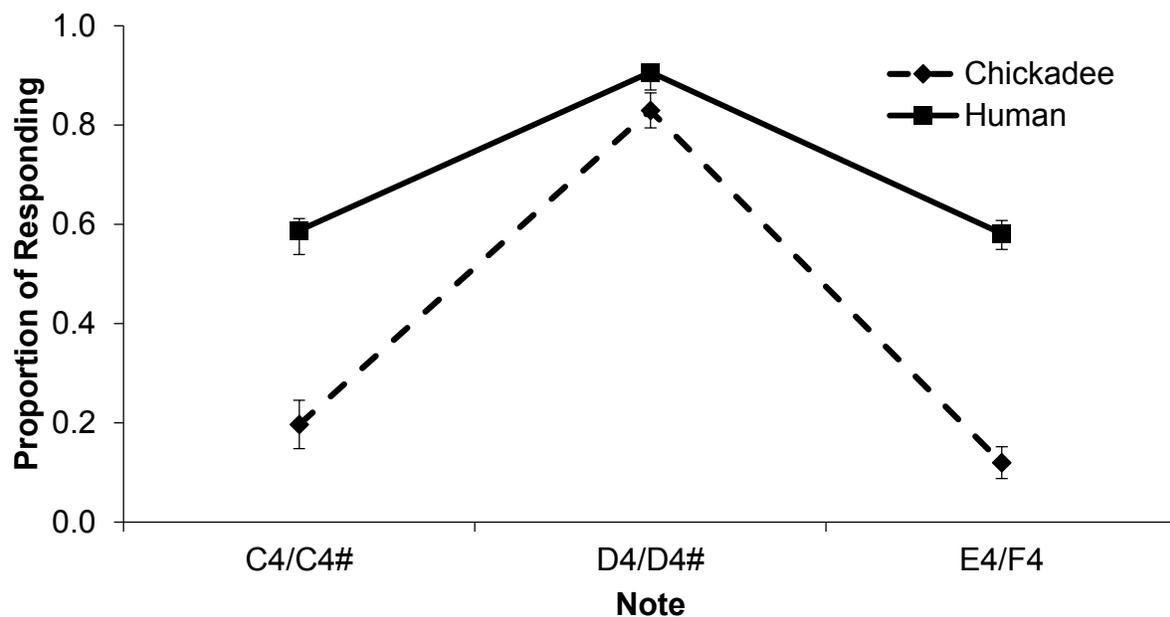
Figure 4.1. Comparison of Discrimination training

Figure 4.1. Comparison of Discrimination training. Figure depicts the responses for humans and chickadees in a go/no-go discrimination task using three note pairs from the 4th octave. The solid line represents the human responses. The dashed line represents the chickadee response. Error bars are \pm S.E.M.

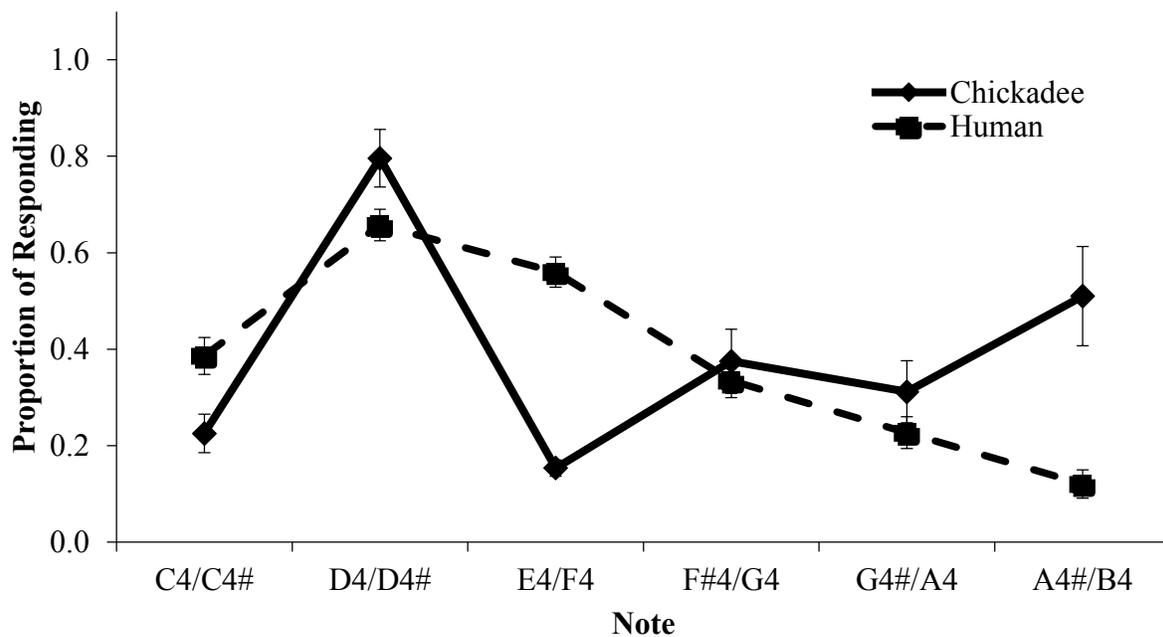
Figure 4.2. Comparison of Intra-octave Generalization testing

Figure 4.2. Comparison of Intra-octave Generalization testing. Figure depicts the responses for humans and chickadees in a generalization task using six note pairs from the 4th octave. The solid line represents the human responses. The dashed line represents the chickadee response. Error bars are \pm S.E.M.

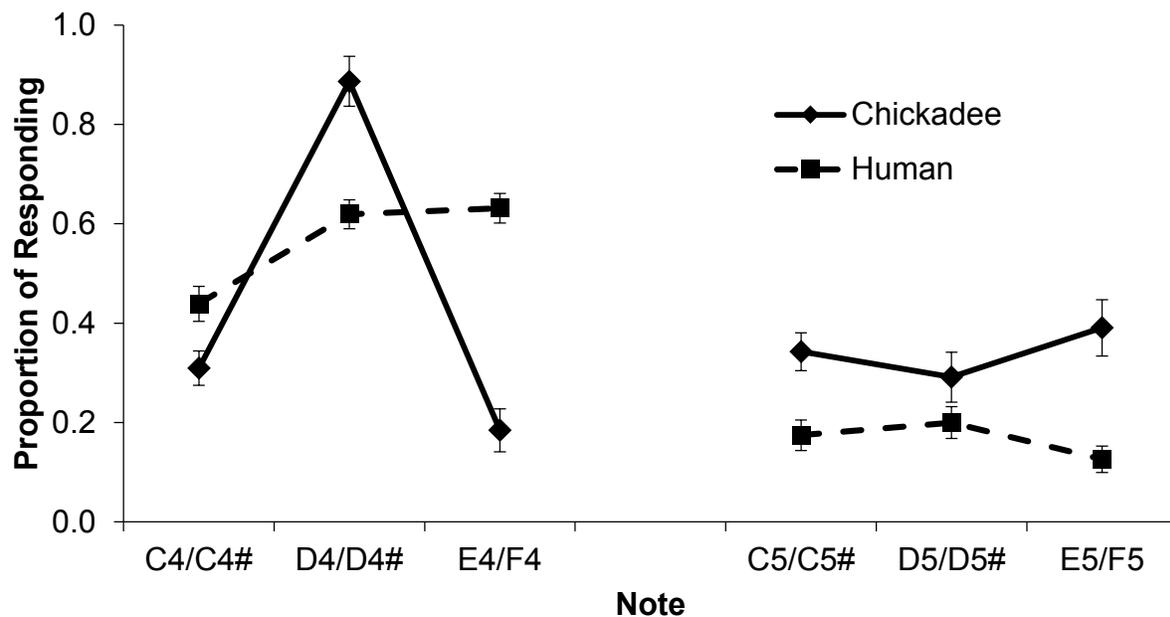
Figure 4.3. Comparison of Inter-octave Generalization testing

Figure 4.3. Comparison of Inter-octave Generalization testing. Figure depicts the responses for humans and chickadees in a generalization task using three note pairs from the 4th octave and three note pairs from the 5th octave. The solid line represents the human responses. The dashed line represents the chickadee response. Error bars are \pm S.E.M.

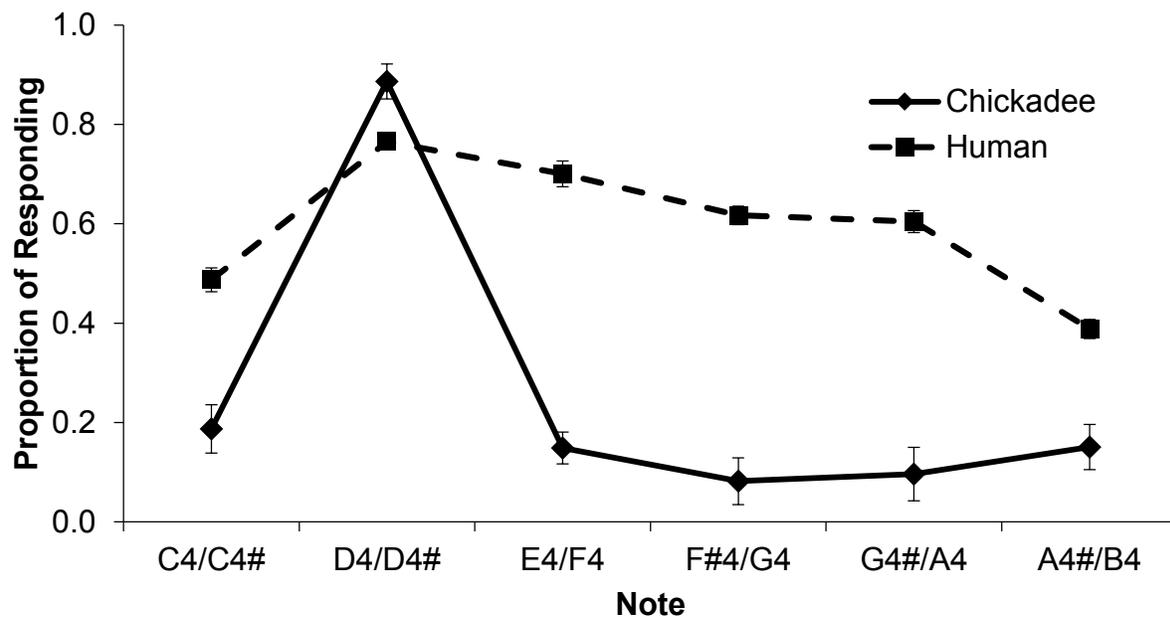
Figure 4.4. Comparison of Intra-octave Original-transfer testing

Figure 4.4. Comparison of Intra-octave Original-transfer testing. Figure depicts the responses for humans and chickadees in the Transfer testing task using six note pairs from the 4th octave. The solid line represents the human responses. The dashed line represents the chickadee response.

Error bars are \pm S.E.M.

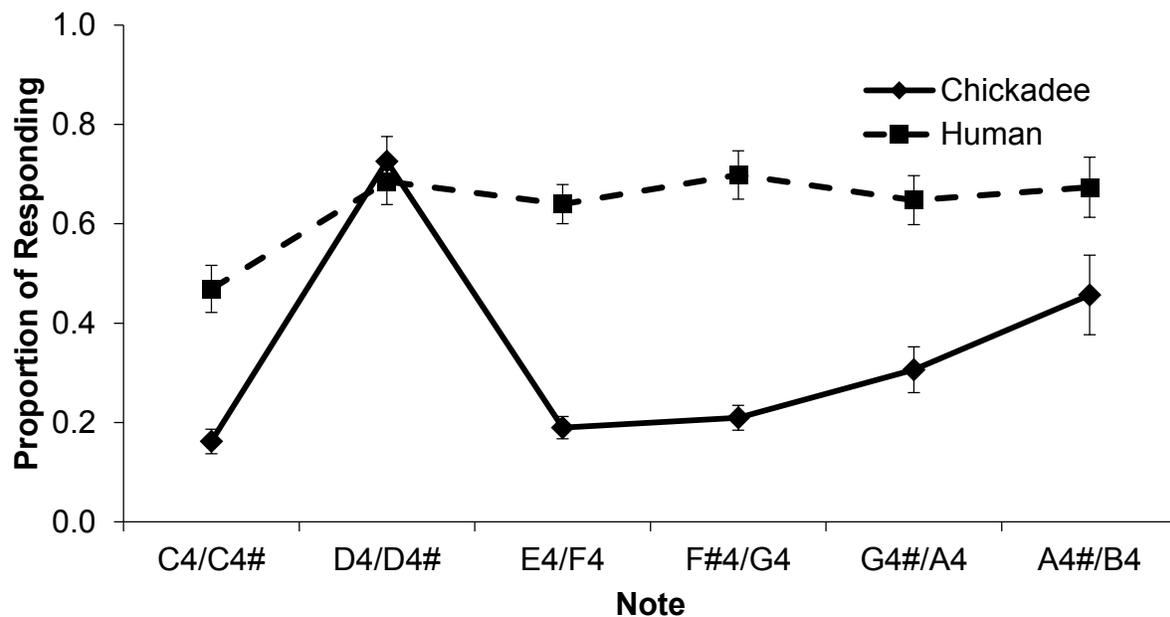
Figure 4.5. Comparison of Intra-octave Partial-reversal Transfer testing

Figure 4.5. Comparison of Intra-octave Partial-reversal transfer testing. Figure depicts the responses for humans and chickadees in the Transfer testing task using six note pairs from the 4th octave. The solid line represents the human responses. The dashed line represents the chickadee response. Error bars are \pm S.E.M.

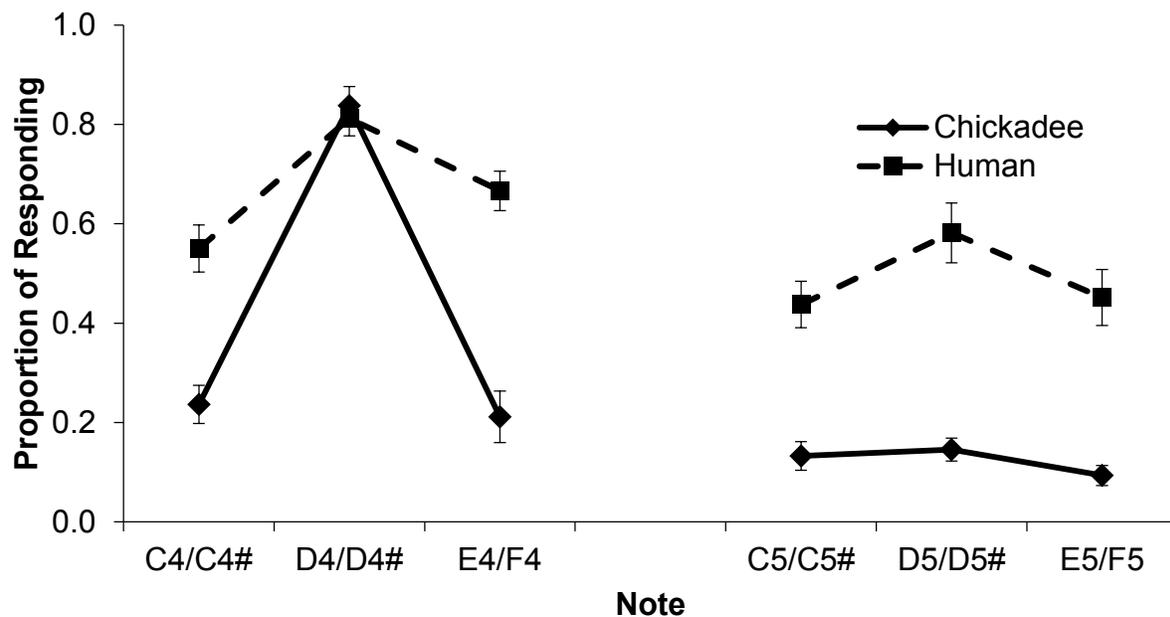
Figure 4.6. Comparison of Inter-octave Original-transfer testing

Figure 4.6. Comparison of Inter-octave Original-transfer testing. The figure depicts the responses for humans and chickadees in the Transfer testing task using three note pairs from the 4th octave and three note pairs from the 5th octave. The solid line represents the human responses. The dashed line represents the chickadee response. Error bars are \pm S.E.M.

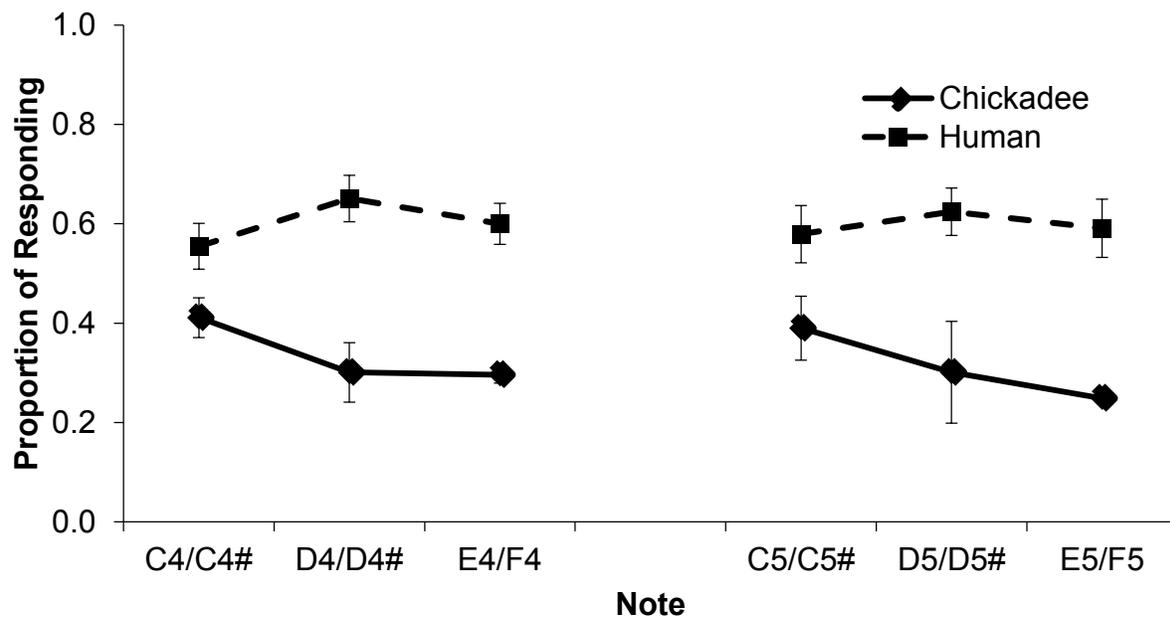
Figure 4.7. Comparison of Inter-octave Partial-reversal Transfer testing

Figure 4.7. Comparison of Inter-octave Partial-reversal Transfer testing. The figure depicts the responses for humans and chickadees in the Transfer testing task using three note pairs from the 4th octave and three note pairs from the 5th octave. The solid line represents the human responses. The dashed line represents the chickadee response. Error bars are \pm S.E.M.

References

- Allen, D. (1967). Octave discriminability of musical and non-musical subjects. *Psychonomic Science*, 7(12), 421-422.
- Athos, E. A., Levinson, B., Kistler, A., Zemansky, J., Bostrom, A., Freimer, N., & Gitschier, J. (2007). Dichotomy and perceptual distortions in absolute pitch ability. *Proceedings of the National Academy of Sciences*, 104, 14795–14800. doi:10.1073/pnas.0703868104
- Balkwill, L. L., & Thompson, W. F. (1999). A cross-cultural investigation of the perception of emotion in music: Psychophysical and cultural cues. *Music Perception*, 43-64.
- Butler, J. W., & Daston, P. G. (1968). Musical consonance as musical preference: A cross-cultural study. *The Journal of General Psychology*, 79(1), 129-142.
- Bolhuis, J. J., Tattersall, I., Chomsky, N., & Berwick, R. C. (2014). How could language have evolved?. *PLoS Biology*, 12(8), e1001934.
- Brockway, B. F. (1969). Roles of budgerigar vocalization in the integration of breeding behaviour. *Bird Vocalizations*, 131-158. Cambridge University Press.
- Chomsky, N. (1956). Three models for the description of language. *Information Theory, IRE Transactions on*, 2(3), 113-124.
- Chomsky, N. (1986). *Knowledge of language: Its nature, origin, and use*. Greenwood Publishing Group.

- Crockford, C., Herbinger, I., Vigilant, L., & Boesch, C. (2004). Wild chimpanzees produce group-specific calls: A case for vocal learning? *Ethology*, *110*, 221-243.
- Colombelli-Négrel, D., Hauber, M. E., & Kleindorfer, S. (2014). Prenatal learning in an Australian songbird: habituation and individual discrimination in superb fairy-wren embryos. *Proceedings of the Royal Society B: Biological Sciences*, *281*(1797), 20141154.
- Corballis, M. C. (1992). On the evolution of language and generativity. *Cognition*, *44*(3), 197-226.
- Darwin, C. (1871). *The descent of man and selection in relation to sex*. John Murray. London.
- DeCasper, A. J., & Fifer, W. P. (1980). Of human bonding: Newborn's prefer their mothers' voices. *Science*, *208*, 1174-1176.
- Demany, L., & Armand, F. (1984). The perceptual reality of tone chroma in early infancy. *The Journal of the Acoustical Society of America*, *76*(1), 57-66.
- Doupe, A. J., & Kuhl, P. K. (1999). Birdsong and human speech: common themes and mechanisms. *Annual Review of Neuroscience*, *22*(1), 567-631.
- Dowling, W. J., & Harwood, D. L. (1986). *Music cognition*. Academic Press.
- Egnor, S. R., & Hauser, M. D. (2004). A paradox in the evolution of primate vocal learning. *Trends in Neurosciences*, *27*(11), 649-654.

- Farabaugh, S. M., Linzenbold, A., & Dooling, R. J. (1994). Vocal plasticity in Budgerigars (*Melopsittacus undulatus*): evidence for social factors in the learning of contact calls. *Journal of Comparative Psychology*, *108*(1), 81.
- Fernald, A., Taeschner, T., Dunn, J., Papousek, M., de Boysson-Bardies, B., & Fukui, I. (1989). A cross-language study of prosodic modifications in mothers' and fathers' speech to preverbal infants. *Journal of Child Language*, *16*, 477-501.
- Fitch, W. T. (2005). The evolution of music in comparative perspective. *Annals of the New York Academy of Sciences*, *1060*(1), 29-49.
- Fitch, W. T. (2006). The biology and evolution of music: A comparative perspective. *Cognition*, *100*(1), 173-215.
- Fitch, W. T. (2013). Musical protolanguage: Darwin's theory of language evolution revisited. Bolhuis, J. J., & Everaert, B. (Eds.), *In Birdsong, speech, and language: Exploring the evolution of mind and brain*. Cambridge: MIT Press.
- Garamszegi, L. Z., Pavlova, D. Z., Eens, M., & Møller, A. P. (2007). The evolution of song in female birds in Europe. *Behavioral Ecology*, *18*, 86-96.
- Hahn, A. H., Guillette, L. M., Lee D., Hoang, J., McMillan N., Sturdy C. B. (2015). Experience affects immediate early gene expression in response to conspecific call notes in black-capped chickadees (*Poecile atricapillus*). *Behavioural Brain Research*, *287*, 49-58.
doi:10.1016/j.bbr.2015.03.021

- Hauser, M. D., & McDermott, J. (2003). The evolution of the music faculty: A comparative perspective. *Nature Neuroscience*, 6(7), 663-668.
- Hearst, E., Koresko, M. B., & Poppen, R. (1964). Stimulus generalization and the response-reinforcement contingency. *Journal of the Experimental Analysis of Behavior*, 7(5), 369-380.
- Hodun, A., Snowdon, C. T., & Soini, P. (1981). Subspecific Variation in the Long Calls of the Tamarin, *Saguinus fuscicollis*. *Zeitschrift für Tierpsychologie*, 57(2), 97-110.
- Hoeschele, M., Weisman, R. G., & Sturdy, C. B. (2012). Pitch chroma discrimination, generalization, and transfer tests of octave equivalence in humans. *Attention, Perception, & Psychophysics*, 74(8), 1742-1760.
- Hoeschele, M., Weisman, R. G., Guillette, L. M., Hahn, A. H., & Sturdy, C. B. (2013). Chickadees fail standardized operant tests for octave equivalence. *Animal Cognition*, 16, 599-609.
- Honing, H., Merchant, H., Háden, G. P., Prado, L., & Bartolo, R. (2012). Rhesus monkeys (*Macaca mulatta*) detect rhythmic groups in music, but not the beat. *PloS One*, 7(12), e51369.
- Hughes, M., Nowicki, S., & Lohr, B. (1998). Call learning in black-capped chickadees (*Parus atricapillus*): The role of experience in the development of 'chick-a-dee' calls. *Ethology*, 104(3), 232-249.

- Hulse, S. H., & Cynx, J. (1985). Relative pitch perception is constrained by absolute pitch in songbirds (*Mimus*, *Molothrus*, and *Sturnus*). *Journal of Comparative Psychology*, *99*(2), 176.
- Hulse, S. H., & Cynx, J. (1986). Interval and contour in serial pitch perception by a passerine bird, the European starling (*Sturnus vulgaris*). *Journal of Comparative Psychology*, *100*(3), 215.
- Hulse, S. H., Bernard, D. J., & Braaten, R. F. (1995). Auditory discrimination of chord-based spectral structures by European starlings (*Sturnus vulgaris*). *Journal of Experimental Psychology: General*, *124*(4), 409.
- Izumi, A. (2000). Japanese monkeys perceive sensory consonance of chords. *The Journal of the Acoustical Society of America*, *108*(6), 3073-3078.
- Janik, V. M., & Slater, P. B. (1997). Vocal learning in mammals. *Advances in the Study of Behavior*, *26*, 59-99.
- Jarvis, E. D. (2004). Learned birdsong and the neurobiology of human language. *Annals of the New York Academy of Sciences*, *1016*, 749-777.
- Kallman, H. J. (1982). Octave equivalence as measured by similarity ratings. *Perception & Psychophysics*, *32*(1), 37-49.
- Kishon-Rabin, L., Amir, O., Vexler, Y., & Zaltz, Y. (2001). Pitch discrimination: Are professional musicians better than non-musicians? *Journal of Basic and Clinical Physiology and Pharmacology*, *12*(2), 125-144.

- Lemasson, A., Ouattara, K., Petit, E. J., & Zuberbühler, K. (2011). Social learning of vocal structure in a nonhuman primate? *BMC Evolutionary Biology*, *11*(1), 362.
- Lieberman, P., Klatt, D. H., & Wilson, W. H. (1969). Vocal tract limitations on the vowel repertoires of rhesus monkey and other nonhuman primates. *Science*, *164*(3884), 1185-1187.
- MacDougall-Shackleton, S. A., & Hulse, S. H. (1996). Concurrent absolute and relative pitch processing by European starlings (*Sturnus vulgaris*). *Journal of Comparative Psychology*, *110*(2), 139.
- Marler, P., & Tamura, M. (1964). Culturally transmitted patterns of vocal behavior in sparrows. *Science*, *146*(3650), 1483-1486.
- Marler, P., & Peters, S. (1982). Structural changes in song ontogeny in the swamp sparrow *Melospiza georgiana*. *The Auk*, *99*, 446-458.
- Masataka, N., & Fujita, K. (1989). Vocal learning of Japanese and rhesus monkeys. *Behaviour*, *109*(3), 191-199.
- Mitani, J. C. (1987). Species discrimination of male song in gibbons. *American Journal of Primatology*, *13*(4), 413-423.
- Mitani, J. C., & Gros-Louis, J. (1998). Chorusing and call convergence in chimpanzees: tests of three hypotheses. *Behaviour*, *135*(8), 1041-1064.

- Miyazaki, K. I. (1988). Musical pitch identification by absolute pitch possessors. *Perception & psychophysics*, 44(6), 501-512.
- Miyazaki, K. I. (1989). Absolute pitch identification: Effects of timbre and pitch region. *Music Perception*, 7, 1-14.
- Nazzi, T., Floccia, C., & Bertoncini, J. (1998). Discrimination of pitch contours by neonates. *Infant Behavior and Development*, 21(4), 779-784.
- Nakagawa, E. (1986). Overtraining, extinction and shift learning in a concurrent discrimination in rats. *The Quarterly Journal of Experimental Psychology*, 38(3), 313-326.
- Njegovan, M., & Weisman, R. (1997). Pitch discrimination in field-and isolation-reared black-capped chickadees (*Parus atricapillus*). *Journal of Comparative Psychology*, 111(3), 294.
- Nowicki, S. (1989). Vocal plasticity in captive black-capped chickadees: the acoustic basis and rate of call convergence. *Animal Behaviour*, 37, 64-73.
- Nottebohm, F. (1972). The origins of vocal learning. *American Naturalist*, 106, 116-140.
- Plantinga, J., & Trainor, L. J. (2005). Memory for melody: Infants use a relative pitch code. *Cognition*, 98(1), 1-11.
- Searcy, W. A., Anderson, R. C., & Nowicki, S. (2006). Bird song as a signal of aggressive intent. *Behavioral Ecology and Sociobiology*, 60(2), 234-241.

- Sergeant, D., & Roche, S. (1973). Perceptual shifts in the auditory information processing of young children. *Psychology of Music*, 1(2), 39-48
- Shackleton, S. A., & Ratcliffe, L. (1993). Development of song in hand-reared black-capped chickadees. *The Wilson Bulletin*, 105, 637-644.
- Shepard, R. N. (1982). Geometrical approximations to the structure of musical pitch. *Psychological Review*, 89, 305–333.
- Snowdon, C. T., & Elowson, A. M. (1999). Pygmy marmosets modify call structure when paired. *Ethology*, 105(10), 893-908.
- Stevens, C. (2004). Cross-cultural studies of musical pitch and time. *Acoustical Science and Technology*, 25(6), 433-438.
- Spence, M. J., & Freeman, M. (1996). Newborn infants prefer the maternal low-pass filtered voice, but not the maternal whispered voice. *Infant Behavior and Development*, 19, 199-212.
- Talmage-Riggs, G., Winter, P., Ploog, D., & Mayer, W. (1972). Effect of deafening on the vocal behavior of the squirrel monkey (*Saimiri sciureus*). *Folia Primatologica*, 17(5-6), 404-420.
- Trehub, S. E. (2000). Human processing predispositions and musical universals. Nils, W. L., Merker, B., & Brown, S. (Eds.), *The Origins of Music* (427-448). MIT press.

- Watanabe, S., Uozumi, M., & Tanaka, N. (2005). Discrimination of consonance and dissonance in Java sparrows. *Behavioural Processes*, 70(2), 203-208.
- Weeden, J. S., & Falls, J. B. (1959). Differential responses of male ovenbirds to recorded songs of neighboring and more distant individuals. *The Auk*, 76, 343-351.
- Weisman, R. G., Balkwill, L. L., Hoeschele, M., Moscicki, M. K., Bloomfield, L. L., & Sturdy, C. B. (2010). Absolute pitch in boreal chickadees and humans: Exceptions that test a phylogenetic rule. *Learning and Motivation*, 41(3), 156-173.
- Winter, P., Handley, P., Ploog, D., & Schott, D. (1973). Ontogeny of squirrel monkey calls under normal conditions and under acoustic isolation. *Behaviour*, 47(3), 230-239.
- Wright, A. A., Rivera, J. J., Hulse, S. H., Shyan, M., & Neiwirth, J. J. (2000). Music perception and octave generalization in rhesus monkeys. *Journal of Experimental Psychology: General*, 129(3), 291.
- Vaughan, W. (1988). Formation of equivalence sets in pigeons. *Journal of Experimental Psychology: Animal Behavior Processes*, 14(1), 36.
- Vicario, D. S., Naqvi, N. H., & Raksin, J. N. (2001). Sex differences in discrimination of vocal communication signals in a songbird. *Animal Behaviour*, 61(4), 805-817.
- Zentner, M. R., & Kagan, J. (1998). Infants' perception of consonance and dissonance in music. *Infant Behavior and Development*, 21(3), 483-492.

Zentall, T. R., Steirn, J. N., Sherburne, L. M., & Urcuioli, P. J. (1991). Common coding in pigeons assessed through partial versus total reversals of many-to-one conditional and simple discriminations. *Journal of Experimental Psychology: Animal Behavior Processes*, 17(2), 194.