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Comparative Study of Beat and Temporal Pattern Perception in a Songbird

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Abstract

When humans listen to musical rhythms they sense a beat, the regular pulse that one might tap their foot to. Much about the functions, evolution and neural substrates of beat perception remains unclear. Research has considered whether other species perceive beat, yet more empirical data is needed. Songbirds produce learned rhythmic vocalizations, but can they perceive a beat? To answer this question, I developed a behavioural task that tested whether humans could discriminate rhythms that contained or lacked a beat. I applied an equivalent procedure to test European starlings. I found that humans learned the task with minimal instructions, but starlings were unable to discriminate on the basis of beat presence. Additional testing revealed that the starlings used absolute timing cues and ignored global patterns in rhythms. This work contributes a paradigm that may be adapted to study other species. Its results provide insight for designing future comparative rhythm experiments.

Keywords

European starling, beat perception, rhythm, comparative, auditory discrimination, implicit attention, music, temporal processing

Co-Authorship Statement

I performed the work in this thesis under the co-supervision of Dr. Scott MacDougall-Shackleton and Dr. Jessica Grahn. Dr. Molly Henry contributed ideas that precipitated this research and provided helpful support with experimental design and programming. Versions of the second and third chapters of this thesis will be published with these three individuals included as co-authors.

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This last section is for the birds. I am better for receiving the unconditional love of my feathered family of pet parrots: Lester, Big Bird, Petri and Beau, whose antics first sparked my interest in avian cognition, and who patiently shared me with other birds for a time. Working daily with 15 starlings over the course of a year greatly improved my appreciation of animal behaviour, in all its wildness. Though starlings are commonly regarded as pests, these birds have imparted me with an appreciation for their remarkable intelligence and beauty.

I am told that the winding path to academic success must sometimes be followed through patches of darkness. For those moments, here I leave a note to remind myself of where the path met light.

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Chapter 1

1 Introduction

In its waking state the brain works continuously to detect patterns as it processes sensory input from the environment. By identifying a pattern of events that unfolds over time, the brain may extract temporal information and use it to predict the timing of events into the future. The capacities of humans to perceive temporal patterns in the auditory domain is fundamental to cognition of speech and music. Of interest to this thesis are patterns that emerge from the temporal features of rhythm and make humans want to move to them.

1.1 Perception of Rhythm and Beat

Music has been defined as an organization of sound that spans across time (Cage, 1961; Varese and Wen-chung, 1966). In music humans will often sense a beat: a periodic isochronous pulse that is experienced internally and derives from the timing of sounds and silences in a rhythm (Cooper and Meyer, 1960). A series of beats defines meter, the timing framework which organizes the series into repeating patterns of regular stressed and unstressed beats (Large, 2008; Lerdahl & Jackendoff, 1983). An induced beat pattern is perpetuated as the listener anticipates future beats and predicts that regularly recurring events in rhythms will fall on the beat (Rankin et al., 2009). A sense of beat often emerges from the perception of variations across multiple physical properties of music, such as the frequency and spectrum of notes. As described by Kung, Chen, Zatorre and Penhune (2013): “musical beat has no one-to-one relationship with auditory features—it is an abstract perceptual representation that emerges from the interaction between sensory cues and higher level cognitive organization”.

The beat may be identified as the point in time when humans will align their movements to sound (Drake et al., 2000a). Induction of bodily movement is considered a universal feature of musicality common to every culture in the world (Brown & Jordania, 2013). The ability to match the timing of movement to beat, referred to as entrainment or synchronization, is essential for dance and musical performance. Humans will spontaneously synchronize the timing of repetitive movement (i.e., clapping, nodding, finger or foot tapping, etc.) to the beat of music, and doing so has been shown to aid in finding a beat (Su & Pöppel, 2012).

Before I proceed further, I wish to clarify some of the terminology that is referenced throughout this document. In the rhythm cognition literature, authors vary widely in their usage of terms to represent certain characteristic features of music. Without providing clear definitions, it can be tricky to interpret terminology that holds alternate meanings and to compare between works on such abstract topics (Fitch, 2013). As it pertains to this thesis, *rhythm* simply refers to any stream of discrete intervals of time. Humans will mentally fit rhythms to *meter* or *metrical structure*, a hierarchical framework that predicts the position of stress/accents (as in speech and music). An *accent* is an instance when a note onset is emphasized or particularly salient relative to its neighbors. I use the term *perception* to describe both processes by which a listener senses acoustic features of a rhythm (such as pitch perception) and other processes wherein the listener encodes a rhythm through some psychological organization (i.e., in the perception of regularity, accents or meter). Here the term *beat* describes the regular internal pulse that is experienced by humans while listening to a rhythm. I use the term *induction* to relate the perception of temporally regular accents to the emergence of a beat (as in Povel and Essens, 1985, discussed below).

1.1.1 Models of Beat Perception

Humans' perception of rhythm has been modelled extensively, and much of this work has concentrated on beat and meter (Desain, 1992; Longuet-Higgins & Lee, 1982; Parncutt, 1994; Steedman, 1977). In general, models predict that the ease with which a beat may be found in a piece of music depends on temporal regularity in the sound. Two alternate schools of thought consider either a metrical (beat-based) coding of rhythm (Essens & Povel, 1985; Povel & Essens, 1985) or figural coding that is determined by grouping principles (Hébert & Cuddy, 2002). Some models are defined by rules that the brain uses to impose metrical structure and accents onto a rhythm (Povel & Okkerman, 1981) while others focus on the entrainment of internal oscillatory processes to periodicities in rhythm (e.g., Large & Jones, 1999; Large & Palmer, 2002).

One prominent model of metrical coding is that of Povel & Essens (1985). To briefly summarize the model, the distribution of accents that a listener perceives while listening to rhythm is decided by a set of rules, and regularities in this distribution are related to the induction of a beat. A sense of beat may emerge when the listener mentally compares the position of these accents with the isochronous units of a regular internal clock. The fit of accents to the clock predicts the strength of the beat, and the unit of the clock decides the rate of the beat. In this thesis I design auditory rhythms based on the Povel & Essens model and present them to human participants and animal subjects in a series of behavioural experiments. A more detailed breakdown of the model and description of these stimuli are provided in the second Chapter.

1.1.2 Neuroscience of Beat

Most of the early experimental research on beat perception and production ability concentrated on synchronization of tapping with auditory sequences (e.g., Duke, 1989, 1994; Dunlap, 1910; Parncutt, 1994; see Repp, 2005 for a comprehensive review of the tapping

literature). In recent years a broader variety of behavioural tasks have been developed for testing beat perception, including those that measure production of movement in synchrony with beat and others that probe beat perception more directly (e.g., Fujii & Schlaug, 2013; Iversen & Patel, 2008). These tasks have been used in several investigations into factors that underlie large individual differences in beat perception and production (Grahn & McAuley, 2009; Musil et al., 2014; Nozaradan et al., 2016). Perception of beat is profoundly influenced by exposure to music and cultural differences in musical conventions (Cameron et al., 2015; Creel, 2012; Jacoby and McDermott, 2017; Polak et al., 2018), though humans are sensitive to beat early in development (Hannon & Trehub, 2005). Many studies have specifically looked at how beat perception ability is shaped by past musical experiences and training, and differences have been found between the performance of beat-based tasks by musical experts (i.e., musicians) and non-experts (e.g., Bouwer et al., 2018; Cameron & Grahn, 2014; Duke et al., 1991; Vuust et al., 2005).

In recent years progress has been made towards identifying the neural substrates of beat perception. Advances in neuroimaging have allowed researchers to map the human brain's facilities for perceiving and producing rhythms. Using functional magnetic resonance imaging (fMRI) many studies have observed patterns of neural activity during beat processing tasks that overlap heavily with patterns observed during timing tasks. These include areas associated with the motor system: premotor cortex, supplementary motor area, cerebellum, and the basal ganglia (Bengtsson et al., 2009; Chen et al., 2008; Grahn & Brett, 2007; Grahn & Rowe, 2013; Lewis et al., 2004; Mayville et al., 2002; Schubotz, 2001; Ullén et al., 2003). A growing body of neuroimaging data supports the idea that beat perception depends upon interactions between the auditory and motor systems (Chen et al., 2006; Grahn & Rowe, 2009). Furthermore, techniques in electrophysiology have been developed that afford greater temporal resolution for examining

patterns of neural activation in response to auditory stimulation. Electroencephalography (EEG) and magnetoencephalography (MEG) have both been used successfully to characterize neural components associated with meter and rhythm processing (Iversen et al., 2009; Snyder & Large, 2005).

Even with all these exciting developments, the scope of experimental research on beat perception in humans is necessarily limited by obvious ethical restrictions of methodology that can be carried out with human participants. Fortunately, through comparative research, it is possible to further our understanding of cognitive processes in humans by studying the brains and behaviour of other species. Examining the distribution of musical capacities and traits across species may teach us about their evolutionary history (McDermott & Hauser, 2005). An animal model of beat perception would enable more invasive approaches to be tried in research, such as manipulations of a subject's experiences across development (e.g., Fehér et al., 2009), the application of brain lesions (e.g., Bottjer et al., 1984) or the use of intracranial recording techniques for localizing neural activity in an anaesthetized or even awake subject (e.g., Schall et al., 2015). In the third Chapter of this thesis I explore the feasibility of a songbird model of beat perception.

1.2 Cross-Species Studies of Beat Perception

A sense of timing is vital to fitness for all animals. The interactions between an animal and its environment unfold over time, and an animal's perception of time can greatly influence its success. For predators and prey, timing of movement can make the difference between a meal or evasion; for social animals, timing is essential for communication. Social animals transmit signals to each other with their behaviour and many signals are inherently temporal. The synchronous flashes of fireflies (Buck, 1988), the chirping of crickets (Greenfield, 1994) and the

competitive croaking of frogs (Klump & Gerhardt, 1994) are all examples in which proper timing is necessary for a signal to be communicated effectively to conspecifics. However, these behaviours are found in neurologically simple animals and are thought to require only rudimentary cognitive processes that are largely automatic (Wilson & Cook, 2016). When the communication of an animal is more sophisticated, as in spoken language or birdsong, the temporal features of a signal may convey rich, meaningful information.

Many animals can vocalize, but few are capable of modifying their vocal repertoire with experience. Imitative vocal learning is thought to occur in only five groups of mammals (humans, cetaceans, elephants, bats and seals) and three groups of birds (songbirds, parrots, and hummingbirds) (Nottebohm, 1972; Janik & Slater, 1997; Nowicki & Searcy, 2014). Vocal learning is widely accepted as a rare ability. However, the criteria that may be used to define a vocal behaviour as evidence for vocal learning in a given species are not clearly defined in the literature. Additional to the groups listed above, some authors have argued that vocal learning may also occur in some species which show a lesser degree of vocal flexibility – despite being conventionally labeled as non-learners – such as the highly vocal marmoset monkey (e.g., Takahashi et al., 2017). Communication among vocal learning groups can be elaborate, and vocal learning species possess specialized brain adaptations for orchestrating their vocalizations (reviewed by Petkov & Jarvis, 2012). The striatal and pallial subdivisions of the cerebrum contain neural structures that are required for vocal learning and bear some homologies between mammals and birds (Jarvis et al., 2005), although the pallium's cortical form in mammals and nuclear form in birds complicate direct comparisons between these groups (Jarvis, 2007). In the three avian groups, though best characterized in songbirds and parrots, these systems include several telencephalic vocal nuclei and other thalamic nuclei. Humans and birds share forebrain

pathways that contribute to vocal learning. Two pathways have been anatomically and functionally distinguished: a posterior pathway for vocal production (Nottembohm, 1976; Simpson, 1990) and an anterior pathway for vocal imitation and plasticity (i.e., learning) (Jarvis, 2004). Together these pathways form a pallial-basal ganglia-thalamic loop that resembles networks associated with speech production in the human brain (Chakraborty & Jarvis, 2015) (Figure 1.0) Vocal learning is thought to critically depend on inputs from the auditory and motor systems, and some theories consider vocal learning to have evolved from specialization of existing motor structures (Feenders et al., 2008).

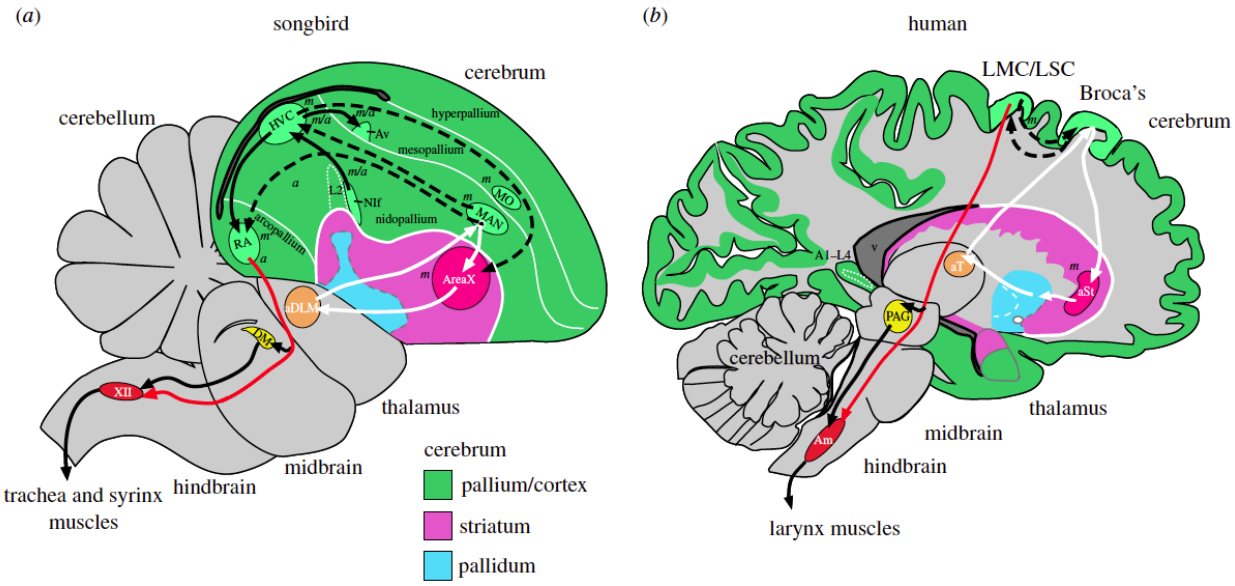

Figure 1.0. Vocal learning and motor pathways for controlling song production in songbirds and spoken language in humans (adapted from Chakraborty & Jarvis, 2015, Figure 1). Black arrows depict the posterior vocal motor pathway; white arrows depict the anterior vocal learning pathway. Connections between these two pathways are depicted with dotted black arrows. Not all structures and connections are shown for simplicity. See Chakraborty & Jarvis (2015) for the full figure legend.

The vocal learning and rhythmic synchronization hypothesis – referred to herein as vocal learning hypothesis – predicts that the capacity of an animal to perceive beat and potentially synchronize its behaviour to beat is restricted to species that learn their vocalizations (Patel, 2006). The hypothesis considers beat perception to be a byproduct of selection for traits that were necessary for vocal learning to evolve. In both the induction of a beat while listening to rhythm and in the process of learning a novel vocalization from the environment, the auditory and motor systems of the brain must be tightly coordinated to facilitate precisely-timed motor responses to auditory stimulation. Although a number of perspectives have been offered on this topic, the nature of the relationship between vocal learning and beat perception ability is not clearly defined in the literature. Some authors have speculated that vocal learning may predispose animals to life experiences early in development that are necessary for beat perception ability to emerge (Schachner, 2013). Others have considered the relevance of factors that may influence an animal's motivation to entrain their movement to sound, including the artificiality of laboratory-based testing (Hoeschele et al., 2015) and whether a rhythmic stimulus is social in nature (Wilson & Cook, 2015). I discuss some of these ideas in the fourth chapter of this thesis.

What do animals perceive in music? In *The Descent of Man* Charles Darwin argued that humans' love of music is evolutionarily ancient and that other animals may also perceive musical cadences and rhythm (Darwin, 1888). Darwin went so far as to speculate that music perception depends on physiological traits shared by the nervous systems of other species. Scientific interest in the possibility of motor entrainment to a beat in non-human animals began over a century ago (Craig, 1916; Wheeler, 1917) but since then only a limited amount of supporting evidence has been found. Although many animals have the ability to time intervals, the consensus among

recent reviews of the comparative rhythm literature is that most species lack the capacity to synchronize their movements with sounds (Bispham, 2006; Hoeschele et al., 2015). Sensitivity to beat is regarded as rare among other animals and likely restricted to a small number of species. Among vocal learning groups, positive experimental evidence for beat perception ability has only been produced in a few individual captive birds, including an Eleonora cockatoo (*Cacatua galerita eleonora*) (Patel et al., 2009) and two parrot species, namely budgerigars (*Melopsittacus undulatus*) (Hasegawa et al., 2011) and grey parrots (*Psittacus erithacus*) (Schachner et al., 2009).

The vocal learning hypothesis also predicts that vocal non-learning primates lack the capacity to perceive auditory beat, despite their phylogenetic closeness to humans. The rhythmic capabilities of other apes and monkeys are the subject of ongoing research and debate (Merchant & Honing, 2014; Patel, 2014) but there is experimental evidence to at least suggest that other primates perceive rhythm quite differently from humans (Honing et al., 2012; Zarco et al., 2009). There is also a paucity of positive evidence for beat perception in vocal non-learning species that have been domesticated and spend time in close proximity to humans, such as horses and dogs (Bregman et al., 2013; Fitch, 2013). Studies of vocal non-learning birds, such as African penguins (*Spheniscus demersus*) (Fobe et al., 2017) and pigeons (*Columba liva*) (Hagmann & Cook, 2010) have found these species to generally lack sensitivity to rhythmicity. This combination of evidence from both vocal learning and non-learning groups has maintained the vocal learning hypothesis as a leading explanation for the distribution of beat perception ability across the animal kingdom. However, the hypothesis was recently challenged by reports of accurate synchronization to an auditory beat by a vocal non-learning species of sea lion (Cook et al., 2013). Further research is needed to confirm whether predictions of the vocal learning

hypothesis are met by other vocal learning and non-learning groups in which beat perception ability has not yet been tested.

1.3 Considerations for Non-Human Animal Experiments

1.3.1 Use of Musical Stimuli

Multiple lines of cross-species research have examined motor synchronization to an auditory beat in clips of Western music. Musical stimuli might be appropriate for exploring other animals' basic capacities for auditory processing, learning and memory. Studies have examined music perception in primates, rodents, birds, fish (reviewed by Watanabe and Kuczaj, 2012) and recently even in reptiles (Behroozi et al., 2018). In some cases, music has been used to enable research that pursues a mechanistic understanding of human musicality by comparatively examining the perception of music by other species. I considered three practical limitations on the utility of music for studying motor entrainment and if/how beat is processed in the brains of other animals.

First, there is the acoustic complexity of rhythmic music. The metrical structure of music is typically hierarchical and may contain multiple nested patterns (Brown & Jordania, 2013). Training a subject to attend towards a specific regularity in an auditory stimulus as complex as music would likely require many incremental transfers from simpler stimuli. A non-human animal subject may struggle to perceptually distinguish overlapping features of music. For example, the regular temporal accents in Western music that are thought to contribute to the sense of auditory beat are often accompanied in time by periodic deviations in the pitch, timbre or amplitude of notes (Ellis & Jones, 2009). It would be difficult to convey the requirement of detecting temporal accents in musical stimuli with this extra variation embedded in the sound, and likely impossible to tease apart a subject's perception of these accents given what little is

known about auditory processing in most species. For inferences to be made about what non-human animals perceive in music it is necessary to establish how the brains of other species process the individual rudiments of music, such as meter and melody.

Secondly, just as music is enjoyed subjectively by humans, other animals may have their own individual preferences for particular musical forms, or perhaps more generally, preferred rates or other acoustic qualities such as pitches and timbres (Chiandetti & Vallortigara, 2011; McDermott & Hauser, 2007). It is conceivable that a non-human animal might also conversely experience dislike for certain variations of these features or whole pieces of music, and that their subjective preferences may influence behavioural responding to musical stimuli.

Lastly, to study how animals respond towards human music is anthropocentric. It entails projecting a human construct (music) onto other species to which it is entirely foreign. Comparative research on music cognition must take care not to commit anthropomorphic assumptions about auditory processing in other species. The perceptual sensitivities of other animals may not be compatible with the acoustic qualities of music, which is designed to suit human hearing and preferences. For instance, in some vocal-learning animals, like bats and cetaceans, vocal communication occurs at frequencies beyond humans' audible thresholds. In a series of behavioural experiments Dooling et al. (2002) showed that three species of songbird were able discriminate the temporal fine structure of harmonically complex sounds with resolution approximately two to three times better than the limits shown for humans. Furthermore, the vocalizations of some songbirds may take on rates that are much faster than those common in human music (Eens, 1997).

A more valid approach than using music to investigate natural cognitive processes in other animals might be to use more minimal stimuli that are designed to be ecologically suitable for

the tested species. Beat is experienced by humans commonly in response to Western music, but it is also possible to induce a sense of beat in a human listener using simpler rhythmic patterns. Instead of testing beat perception ability in other species with music, recordings of environmental sounds such as conspecific vocalizations, or other plain monotonal elements, may be incorporated into rhythmic auditory stimuli. In this thesis I tested animal subjects with acoustic rhythms that I constructed with pure tones and designed to loosely resemble the frequency and rate of vocalizations of the test species (see Chapter 3, section 3.3.1 for more information about how these stimulus parameters were selected).

1.3.2 Dissociating Beat Perception from Beat Synchronization

The majority of studies on beat perception ability in animals have examined the capacity of a test subject to synchronize the timing of its body movements with a regular stimulus. Yet there are marked inconsistences in the assumptions, methodology and reporting of these studies which have rendered their findings incommensurable. For example, there is vigorous ongoing debate over whether other primates are sensitive to rhythm and beat and what of their perception is shared with humans. Numerous studies have demonstrated that in humans, the auditory system dominates over the visual system in terms of temporal resolution and performance of temporal tapping tasks (Glenberg et al., 1989; Grahn, 2012; Patel et al., 2005; Repp & Penel, 2002). However, the opposite appears to be true in other primates: macaques have been found to entrain their tapping more accurately to visual than acoustic stimuli (Nagasaka et al., 2013; Zarco et al., 2009). Entrainment is thus not necessarily restricted to a single modality in other species. A few studies have documented cases of spontaneous entrainment of self-initiated drumming in a bonobo (*Pan paniscus)* (Large & Gray, 2015) and in chimpanzees (*Pan troglodytes*) (Dufour et al., 2015; Hattori et al., 2013); reports also exist of accurate entrainment of vocal duetting in

gelada monkeys (*Theropithecus gelada*) (Richman, 1978) and bonobos (de Waal, 1988). In contrast, other laboratory-based studies that have trained primate subjects over many sessions to tap to rhythms, including some that recorded brain activity during auditory presentations, have found only limited evidence for entrainment (Zarco et al., 2009; Honing et al., 2012). How can such mixed results be reconciled given the range of differences in these studies? Some authors have put forward thoughtful suggestions for designing future experiments in an objective, standardized manner that properly captures beat perception ability and will hopefully lead to meaningful comparisons (Bregman et al., 2013; Hoeschele et al., 2015), but so far no particular technique, entrainment-based or otherwise, has been applied consistently across species.

Entrainment of motor behaviour is certainly a strong indication that an animal can detect a beat, but it is not necessarily the best or only means of demonstrating that beat perception occurs in other species. From the existing evidence (and for most species a lack thereof) it seems likely that moving along to sounds is not within the natural behavioural repertoires of most animals, and that some rare few have the capacity to be taught to do so with human intervention. But even in the absence of motor entrainment, it is theoretically possible that a species may still be capable of perceiving an auditory beat. Perhaps an animal is unable, due to physical constraints on its body movement, to synchronize its behaviour to a beat in a manner that is overt and measurable by human observers. Rather than tasking the subject with synchronizing to beat, its capacity to perceive beat may be probed directly by evoking responses that reflect perceptual judgements made about beat-based stimuli.

1.4 Overview of Thesis Objectives

The research I have undertaken seeks to compare beat perception across species. In this thesis I develop a novel paradigm for examining the sensitivity of an animal subject to regular accents (the beat) in metrical auditory patterns. I apply this paradigm to test both human participants and songbird subjects. No songbird species are known to spontaneously synchronize their movement to sounds as parrots do, and consequently no positive evidence of beat perception ability in this avian taxon has ever been reported. This thesis is among only a few investigations that have looked at songbirds' perception of acoustic regularity (van der Aa et al., 2015; ten Cate et al., 2016; Hulse et al., 1984). It is the first to examine their perception of accents in metrical structure. Unlike the majority of previous cross-species behavioural studies of beat perception ability, this approach does not require the subject to entrain its body movement to a stimulus, nor does it involve presenting human music to animals. The methodology I report here potentially allows for direct comparisons of beat perception across species and may be standardized for testing other animals in the future.

Here I outline three objectives for this research. In the second Chapter I describe two experiments with human participants. One experiment addresses the first objective: to determine if humans can detect a beat while listening to the auditory rhythms created for these experiments, and to confirm that this task requires beat perception ability. I consider the effect of participants' musical expertise on their performance. In the second experiment I address a second objective: to examine how beat perception is influenced by prior expectations of a beat. This experiment provides ambiguous instructions and requires participants to learn the task implicitly.

In the third Chapter I describe a series of behavioural experiments which aim to achieve a third objective: to investigate beat perception capability in a species of songbird, the European

starling (*Sturnus vulgaris*). Using operant conditioning, I implement a version of the categorization paradigm described in Chapter 2 to test a prediction of the vocal learning hypothesis that songbirds, a vocal learning group, have the capacity to perceive auditory beat. In a first experiment I train songbirds to discriminate between metrical patterns that contain or lack regular temporal accents. I conduct a second operant experiment to probe starlings' perception of temporal patterns more generally, aiming to identify features of temporal patterns that the birds are sensitive towards. I achieve this aim by presenting novel probe stimuli that require the subjects to generalize from a learned set of baseline patterns.

In the fourth and final Chapter I critically discuss the methods and results of these experiments. I consider the cognitive strategies that were used by human participants while performing the discrimination. The discussion reviews the implications of this thesis and frames its findings in the context of existing work on auditory processing in starlings. I conclude the fourth Chapter with suggestions for future comparative research on beat perception in songbirds and other animals.

Chapter 1 References

Bengtsson, S.L., Ullén, F., Ehrsson, H., Hashimoto, T., Kito, T., Naito, E., Forssberg, H., Sadato, N. (2009). Listening to rhythms activates motor and premotor cortices. Cortex *45*, 62–71.

Behroozi, M., Billings, B.K., Helluy, X., Manger, P.R., Güntürkün, O., Ströckens, F. (2018). Functional MRI in the Nile crocodile: a new avenue for evolutionary neurobiology. Proceedings of Biological Sciences *285*.

Bispham, J. (2006). Rhythm in Music: What is it? Who has it? And Why? Music Perception *24*, 125–134.

Bottjer, S.W., Miesner, E.A., Arnold, A.P. (1984). Forebrain lesions disrupt development but not maintenance of song in passerine birds. Science *224*, 901–903.

Bouwer, F.L., Burgoyne, J.A., Odijk, D., Honing, H., Grahn, J.A. (2018). What makes a rhythm complex? The influence of musical training and accent type on beat perception. PLoS One *13*.

Bregman, M.R., Iversen, J.R., Lichman, D., Reinhart, M., Patel, A.D. (2013). A method for testing synchronization to a musical beat in domestic horses (Equus ferus caballus). Empirical Musicology Review *7*, 144.

Brown, S., Jordania, J. (2013). Universals in the world's musics. Psychology of Music *41*, 229–248.

Buck, J. (1988). Synchronous rhythmic flashing of fireflies. Quarterly Review of Biology *63*, 265–289.

Cage, J. (2011). Silence: lectures and writings. Wesleyan University Press.

Cameron, D.J., Grahn, J.A. (2014). Enhanced timing abilities in percussionists generalize to rhythms without a musical beat. Frontiers in Human Neuroscience *8*.

Cameron, D.J., Bentley, J., Grahn, J.A. (2015). Cross-cultural influences on rhythm processing: reproduction, discrimination, and beat tapping. Frontiers in Psychology *6*.

ten Cate, C., Spierings, M., Hubert, J., Honing, H. (2016). Can birds perceive rhythmic patterns? A review and experiments on a songbird and a parrot species. Frontiers in Psychology *7*.

Chakraborty, M., Jarvis, E. D. (2015). Brain evolution by brain pathway duplication. Philisophical Transactions of the Royal Society B 370(1684), 20150056.

Chen, J.L., Zatorre, R.J., Penhune, V.B. (2006). Interactions between auditory and dorsal premotor cortex during synchronization to musical rhythms. NeuroImage *32*, 1771–1781.

Chen, J.L., Penhune, V.B., Zatorre, R.J. (2008). Listening to musical rhythms recruits motor regions of the brain. Cerebral Cortex *18*, 2844–2854.

Chiandetti, C., Vallortigara, G. (2011). Chicks like consonant music. Psychological Science *22*, 1270–1273.

Cook, P., Rouse, A., Wilson, M., Reichmuth, C. (2013). A California sea lion (*Zalophus californianus*) can keep the beat: motor entrainment to rhythmic auditory stimuli in a non vocal mimic. Journal of Comparative Psychology *127*, 412–427.

Cooper, G.W., Meyer, L.B. (1960). The Rhythmic Structure of Music. Chicago: The University of Chicago Press.

Craig, W. (1916). Synchronism in the rhythmic activities of animals. Science *44*, 784–786.

Creel, S.C. (2012). Similarity-based restoration of metrical information: Different listening experiences result in different perceptual inferences. Cognitive Psychology *65*, 321–351.

Darwin, C. (1888). The descent of man and selection in relation to sex (Vol. 1). London. John Murray.

de Waal, F.B. (1988). The communicative repertoire of captive bonobos (*Pan paniscus*) compared to that of chimpanzees. Behaviour *106*, 183–251.

Desain, P. (1992). A (de)composable theory of rhythm perception. Music Perception 9(4), 439-454.

Dooling, R.J., Leek, M.R., Gleich, O., Dent, M.L. (2002). Auditory temporal resolution in birds: discrimination of harmonic complexes. The Journal of the Acoustical Society of America *112*, 748–759.

Drake, C., Penel, A., Bigand, E. (2000). Tapping in time with mechanically and expressively performed music. Music Perception *18*, 1–23.

Dufour, V., Poulin, N., Charlotte Curé, Sterck, E.H.M. (2015). Chimpanzee drumming: a spontaneous performance with characteristics of human musical drumming. Scientific Reports *5*, 11320.

Duke, R.A. (1989). Musicians' perception of beat in monotonic stimuli. Journal of Research in Music Education *37*, 61.

Duke, R.A. (1994). When tempo changes rhythm: the effect of tempo on nonmusicians' perception of rhythm. Journal of Research in Music Education *42*, 27.

Duke, R.A., Geringer, J.M., Madsen, C.K. (1991). Performance of perceived beat in relation to age and music training. Journal of Research in Music Education *39*, 35.

Dunlap, K. (1910). Reaction to rhythmic stimuli with attempt to synchronize. Psychological Review *17*, 399–416.

Eens, M. (1997). Understanding the complex song of the European starling: an integrated ethological approach. Advances in the Study of Behavior. New York, 26, 355-434.

Ellis, R.J., Jones, M.R. (2009). The role of accent salience and joint accent structure in meter perception. Journal of Experimental Psychology: Human Perception and Performance *35*, 264–280.

Essens, P.J., Povel, D.J. (1985). Metrical and nonmetrical representations of temporal patterns. Perception & Psychophysics *37*, 1–7.

Feenders, G., Liedvogel, M., Rivas, M., Zapka, M., Horita, H., Hara, E., Wada, K., Mouritsen, H., Jarvis, E.D. (2008). Molecular mapping of movement-associated areas in the avian brain: a motor theory for vocal learning origin. PLoS One *3*, e1768.

Fehér, O., Wang, H., Saar, S., Mitra, P.P., Tchernichovski, O. (2009). De novo establishment of wild-type song culture in the zebra finch. Nature *459*, 564.

Fitch, W.T. (2013). Rhythmic cognition in humans and animals: distinguishing meter and pulse perception. Frontiers in Systems Neuroscience *7*, 68.

Fobe, I.A., DeLong, C.M., Wilcox, K.T. (2017). An exploration of rhythm perception in African penguins (*Spheniscus demersus)*. The Journal of the Acoustical Society of America *142*, 2503–2503.

Fujii, S., Schlaug, G. (2013). The Harvard Beat Assessment Test (H-BAT): a battery for assessing beat perception and production and their dissociation. Frontiers in Human Neuroscience *7*, 771.

Glenberg, A.M., Mann, S., Altman, L., Forman, T., Procise, S. (1989). Modality effects in the coding reproduction of rhythms. Memory & Cognition *17*, 373–383.

Grahn, J.A. (2012). See what I hear? Beat perception in auditory and visual rhythms. Experimental Brain Research *220*, 51–61.

Grahn, J.A., Brett, M. (2007). Rhythm and beat perception in motor areas of the brain. Journal of Cognitive Neuroscience *19*, 893–906.

Grahn, J.A., McAuley, J.D. (2009). Neural bases of individual differences in beat perception. NeuroImage *47*, 1894–1903.

Grahn, J.A., Rowe, J.B. (2009). Feeling the beat: premotor and striatal interactions in musicians and nonmusicians during beat perception. Journal of Neuroscience *29*, 7540–7548.

Grahn, J.A., Rowe, J.B. (2013). Finding and feeling the musical beat: striatal dissociations between detection and prediction of regularity. Cerebral Cortex *23*, 913–921.

Greenfield, M. (1994). Synchronous and alternating choruses in insects and anurans: common mechanisms and diverse functions. American Zoologist, 34(6), 605-615.

Hagmann, C.E., Cook, R.G. (2010). Testing meter, rhythm, and tempo discriminations in pigeons. Behavioural Processes *85*, 99–110.

Hannon, E.E., Trehub, S.E. (2005). Metrical categories in infancy and adulthood. Psychological Science *16*, 48–55.

Hattori, Y., Tomonaga, M., Matsuzawa, T. (2013). Spontaneous synchronized tapping to an auditory rhythm in a chimpanzee. Scientific Reports, *3*, 1566.

Hasegawa, A., Okanoya, K., Hasegawa, T., Seki, Y. (2011). Rhythmic synchronization tapping to an audio–visual metronome in budgerigars. Scientific Reports *1*, 120.

Hébert, S., Cuddy, L.L. (2002). Detection of metric structure in auditory figural patterns. Perception & Psychophysics *64*, 909–818.

Hoeschele, M., Merchant, H., Kikuchi, Y., Hattori, Y., ten Cate, C. (2015). Searching for the origins of musicality across species. Philosophical Transactions of the Royal Society B: Biological Sciences *370*, 20140094.

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.

Hulse, S.H., Humpal, J., Cynx, J. (1984). Discrimination and generalization of rhythmic and arrhythmic sound patterns by European starlings (*Sturnus vulgaris*). Music Perception: An Interdisciplinary Journal *1*, 442–464.

Iversen, J., Patel, A. (2008). The Beat Alignment Test (BAT): Surveying beat processing abilities in the general population. Proceedings of the 10th International Conference on Music Perception and Cognition. Sapporo, Japan. 465-468.

Iversen, J.R., Repp, B.H., Patel, A.D. (2009). Top-down control of rhythm perception modulates early auditory responses. Annals of the New York Academy of Sciences *1169*, 58–73.

Jacoby, N., McDermott, J.H. (2017). Integer ratio priors on musical rhythm revealed cross-culturally by iterated reproduction. Current Biology 27, 359–370.

Janik, V., Slater, P. J. 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.

Jarvis, E.D., Gunturkun, O., Bruce, L., Csillag, A., Karten, H., Kuenzel, W., Medina, L., Paxinos, G., Perkel, D.J., Shimizu, T., et al. (2005). Avian brains and a new understanding of vertebrate brain evolution. Nature Reviews Neuroscience *6*, 151–159.

Jarvis, E.D. (2007). Neural systems for vocal learning in birds and humans: a synopsis. Journal of Ornithology *148*, 35–44.

Large, E. W. (2008). Resonating to musical rhythm: theory and experiment. The Psychology of Time, 189-232.

Large, E.W., Gray, P.M. (2015). Spontaneous tempo and rhythmic entrainment in a bonobo (*Pan paniscus*). Journal of Comparative Psychology *129*, 317–328.

Large, E.W., Jones, M.R. (1999). The dynamics of attending: how people track time-varying events. Psychological Review 106, 119–159.

Large, E.W., Palmer, C. (2002). Perceiving temporal regularity in music. Cognitive Science *26*, 1–37.

Lerdahl, F., Jackendoff, R. (1983). A generative theory of tonal music. Cambridge: The MIT Press.

Lewis, P.A., Wing, A.M., Pope, P.A., Praamstra, P., Miall, R.C. (2004). Brain activity correlates differentially with increasing temporal complexity of rhythms during initialisation, synchronisation, and continuation phases of paced finger tapping. Neuropsychologia *42*, 1301–1312.

Longuet-Higgins, H.C., Lee, C.S. (1982). The perception of musical rhythms. Perception *11*, 115–128.

Klump, G.M., Gerhardt, H.C. (1992). Mechanisms and function of call-timing in male-male interactions in frogs. In McGregor, P.K. (Eds.), Playback and Studies of Animal Communication. New York. 153–174.

Mayville, J.M., Jantzen, K.J., Fuchs, A., Steinberg, F.L., Kelso, J.A.S. (2002). Cortical and subcortical networks underlying syncopated and synchronized coordination revealed using fMRI. Human Brain Mapping *17*, 214–229.

McDermott, J., Hauser, M.D. (2007). Nonhuman primates prefer slow tempos but dislike music overall. Cognition *104*, 654-668.

McDermott, J., Hauser, M.D. (2005). The origins of music: innateness, uniqueness, and evolution. Music Perception *23*, 29–59.

Merchant, H., Honing, H. (2014). Are non-human primates capable of rhythmic entrainment? Evidence for the gradual audiomotor evolution hypothesis. Frontiers in Neuroscience *7*, 274.

Musil, J.J., Iversen, J.R., Müllensiefen (2014). Measuring individual differences in musical beat alignment perception. Personality and Individual Differences *60*, S35.

Nagasaka, Y., Chao, Z.C., Hasegawa, N., Notoya, T., Fujii, N. (2013). Spontaneous synchronization of arm motion between Japanese macaques. Scientific Reports *3*, 1151.

Nowicki, S., Searcy, W.A. (2014). The evolution of vocal learning. Current Opinion in Neurobiology *28*, 48–53.

Nottebohm, F. (1972). The origins of vocal learning. American Naturalist *106* (947), 116-140

Nottebohm F., Stokes T.M., Leonard C.M. (1976) Central control of song in the canary, *Serinus canarius*. Journal of Comparative Neurology *165*: 457–486.

Nozaradan, S., Peretz, I., Keller, P.E. (2016). Individual differences in rhythmic cortical entrainment correlate with predictive behavior in sensorimotor synchronization. Scientific Reports *6*, 20612.

Parncutt, R. (1994). A perceptual model of pulse salience and metrical accent in musical rhythms. Music Perception *11*, 409–464.

Patel, A.D. (2006). Musical rhythm, linguistic rhythm, and human evolution. Music Perception *24*, 99–104.

Patel, A.D. (2014). The evolutionary biology of musical rhythm: was Darwin wrong? PLOS One Biology *12*, e1001821.

Patel, A.D., Iversen, J.R., Chen, Y., Repp, B.H. (2005). The influence of metricality and modality on synchronization with a beat. Experimental Brain Research *163*, 226–238.

Patel, A.D., Iversen, J.R., Bregman, M.R., Schulz, I. (2009). Experimental evidence for synchronization to a musical beat in a nonhuman animal. Current Biology *19*, 827–830.

Petkov, C.I., and Jarvis, E.D. (2012). Birds, primates, and spoken language origins: behavioral phenotypes and neurobiological substrates. Frontiers in Evolutionary Neuroscience *4*, 12.

Polak, R., Jacoby, N., Fischinger, T., Goldberg, D., Holzapfel, A., London, J. (2018). Rhythmic prototypes across cultures: a comparative study of tapping synchronization. Music Perception 36, 1–23.

Povel, D.J., Essens, P. (1985). Perception of temporal patterns. Music Perception *2*, 411–440.

Povel, D.J., Okkerman, H. (1981). Accents in equitone sequences. Perception & Psychophysics *30*, 565–572.

Rankin, S.K., Large, E.W., Fink, P.W. (2009). Fractal tempo fluctuation and pulse prediction. Music Perception *26*, 401–413.

Repp, B.H. (2005). Sensorimotor synchronization: a review of the tapping literature. Psychonomic Bulletin & Review *12*, 969–992.

Repp, B.H., Penel, A. (2002). Auditory dominance in temporal processing: new evidence from synchronization with simultaneous visual and auditory sequences. Journal of Experimental Psychology: Human Perception and Performance *28*, 1085–1099.

Richman, B. (1978). The synchronization of voices by gelada monkeys. Primates *19*, 569–581.

Schachner, A. (2013). If horses entrain, don't entirely reject vocal learning: an experience-based vocal learning hypothesis. Empirical Musicology Review *7*, 157.

Schachner, A., Brady, T.F., Pepperberg, I.M., Hauser, M.D. (2009). Spontaneous motor entrainment to music in multiple vocal mimicking species. Current Biology *19*, 831–836.

Schall, U., Müller, B.W., Kärgel, C., Güntürkün, O. (2015). Electrophysiological mismatch response recorded in awake pigeons from the avian functional equivalent of the primary auditory cortex: NeuroReport *26*, 239–244.

Schubotz, R.I. (2001). Interval and ordinal properties of sequences are associated with distinct premotor areas. Cerebral Cortex *11*, 210–222.

Simpson H.B., Vicario D.S. (1990) Brain pathways for learned and unlearned vocalizations differ in zebra finches. Journal of Neuroscience *10*, 1541–1556.

Snyder, J.S., Large, E.W. (2005). Gamma-band activity reflects the metric structure of rhythmic tone sequences. Cognitive Brain Research *24*, 117–126.

Steedman, M.J. (1977). The perception of musical rhythm and metre. Perception *6*, 555–569.

Su, Y.H., Pöppel, E. (2012). Body movement enhances the extraction of temporal structures in auditory sequences. Psychological Research *76*, 373–382.

Takahashi, Y.D., Lao, D.A., Ghazanfar, A.A. (2017). Vocal learning via social reinforcement by infant marmoset monkeys. Current Biology *27*, 1844-1852.

Ullén, F., Forssberg, H., Ehrsson, H.H. (2003). Neural networks for the coordination of the hands in time. Journal of Neurophysiology *89*, 1126–1135.

van der Aa, J., Honing, H., ten Cate, C. (2015). The perception of regularity in an isochronous stimulus in zebra finches (*Taeniopygia guttata*) and humans. Behavioural Processes *115*, 37–45.

Varese, E., Wen-chung, C. (1966). The liberation of sound. Perspectives of New Music *5*, 11.

Vuust, P., Pallesen, K.J., Bailey, C., van Zuijen, T.L., Gjedde, A., Roepstorff, A., Østergaard, L. (2005). To musicians, the message is in the meter. NeuroImage *24*, 560–564.

Watanabe, S. (2013). Animal aesthetics from the perspective of comparative cognition. In S. Watanabe & S. Kuczaj (Eds.), The science of the mind. Emotions of animals and humans: comparative perspectives. New York, NY, US, pp. 129–162.

Wheeler, W.M. (1917). The synchronic behaviour of phalangidæ. Science *45*, 189.

Wilson, M., Cook, P.F. (2016). Rhythmic entrainment: why humans want to, fireflies can't help it, pet birds try, and sea lions have to be bribed. Psychonomic Bulletin & Review *23*, 1647–1659.

Zarco, W., Merchant, H., Prado, L., Mendez, J.C. (2009). Subsecond timing in primates: comparison of interval production between human subjects and rhesus monkeys. Journal of Neurophysiology *102*, 3191–3202.

Chapter 2

2 Introduction

Humans are highly perceptive of regularities in rhythmic sounds. Research on the perception of musical rhythm has spanned over a century (Mach, 1887) and numerous perceptual theories of rhythm have been contributed by the fields of music theory, psychology and cognitive science. When presented with rhythmic music humans will often spontaneously sense a beat: an internal pulse that repeats at equally spaced points in time (Drake et al., 2000; Large & Palmer, 2002). Humans can synchronize the timing of their body movement to a beat, and this capacity is considered fundamental to musicality (Large, 2000). Both perception of a beat and production of movement in response to a beat are essential for musical performance and synchronous dance. The origins of humans' sensitivity to the beat remains unclear: when and why did beat perception ability evolve, what are its adaptive functions and how is it accomplished by the brain? There is extensive ongoing research and debate about the nature of beat perception ability, but more empirical data is still needed before research can begin to address these and other important outstanding questions.

Recently there has been renewed interest in the sensitivity of other species to the beat (Hoeschele et al., 2015; Patel & Iversen, 2014; Wilson & Cook, 2016). To recognize how the traits necessary for beat perception are distributed across the animal kingdom, which may tell us something about their evolution in humans, experimental research must span a diverse range of taxa. If research produces evidence that other species can perceive a beat, it may be possible to further study the cognitive processes that underlie beat perception in an animal model. A growing body of work has focussed on the rhythmic capacities of primate species. Given that beat induction is considered universal in humans, shown to be common across cultures (Nettl,

2000) and to emerge early in development (Winkler et al., 2009), it is curious that multiple animal studies have produced results that suggest our closest phylogenetic relatives in other primates process rhythm very differently than we do. Though a couple of reports of accurate motor entrainment to an auditory beat by chimpanzees and bonobos have surfaced in recent years (e.g., Hattori et al., 2013; Large & Gray, 2015) earlier work had found that macaque monkeys were incapable of matching the phase of their tapping with a beat (Zarco et al., 2009). Even more perplexing is that positive experimental evidence for beat perception ability has only been found elsewhere in parrots (Hasegawa et al., 2011; Patel et al., 2009; Schachner et al., 2009) and in an individual sea lion (Cook et al., 2013). Most animal studies on this topic have measured their subjects' capacity for motor entrainment to a beat as a proxy for testing the species' capacity for beat perception. In the human rhythm literature beat perception and beat production (as a measure of motor entrainment) are usually treated as separate cognitive skills; the relationship between the two is a topic of much interest. Yet there are few proven methods for testing beat perception in other animals that don't rely on motor entrainment.

In this thesis I develop a novel behavioural testing paradigm that can be used to examine whether other species can detect an auditory beat. The paradigm consists of a discrimination task in which the subject sorts auditory stimuli into two categories depending on the strength of a beat they may perceive while listening. This method enables direct comparisons between perceptual judgements made about beat-based stimuli by human and non-human animal subjects. In this Chapter I describe an application of this paradigm in two computer-based experiments with human participants. The first aim of these experiments was to verify that the procedure recruits humans' ability to perceive an auditory beat, and to provide a basis to compare performance of

the discrimination by humans with the performance of animal subjects in an equivalent operant experiment described in the third chapter.

2.1.1 Implicit Beat Perception

Some research has considered how perception of rhythm is modulated by temporal orienting of attention. Humans' perception of complex temporal patterns, such as the hierarchically structured regularities of speech and music, is thought to depend upon a combination of lower-level processes that are mostly automatic (for example, perceptual chunking of tones) and higher-level processes that may require voluntary attention (for example, the perception of syntax). A key distinction is made in the timing literature between implicit timing – the use of temporal structure for making subconscious predictions about future durations – and explicit timing – deliberate comparison between a presented duration and a memorized standard. Coull and Nobre (2008) found discrete neural substrates for these two forms of timing using fMRI. In a separate imaging study Rohenkohl et al. (2011) examined how the brain shifts between exogenous and endogenous mechanisms for orienting attention to rhythm. Their findings suggest that similar to orienting of visual spatial attention, the brain uses separate systems for temporal orienting of top-down (explicit) timing and bottom-up (implicit) timing.

Little work has explored implicit awareness of a beat. Temporal anticipation is known to be important for orienting attention in rhythms (Jones, 1976; Jones & Boltz, 1989) but it is unclear how consciously expecting the presence of a beat relates to spontaneous beat induction. For instance, in the absence of clear instruction to listen for a beat, will humans still perceive one? Most behavioural tasks that test beat perception or production instruct subjects beforehand to make them explicitly aware of the presence of a beat (e.g., Fujii & Schlaug, 2013; Iversen &

Patel, 2008). Here I describe two experiments that examine how humans' prior expectations of a beat in auditory rhythms influences their perception of a beat. The two experiments contain identical auditory stimuli and the same testing procedure, differing only in the task instructions that are provided. I compare performance across these experiments in order to determine if humans are as sensitive to a beat implicitly as they are when explicitly instructed to find a beat. I also look at the role of musical expertise in this sensitivity.

In the first experiment, participants received explicit instructions, including a conventional definition of the beat as a regular pulse experienced in music and a clear outline of the requirement of the discrimination: to separate auditory patterns with a stronger beat from those with a weaker beat. In the second experiment, other participants received implicit instructions in which the requirements of the discrimination are ambiguous. The implicit instructions only told the participant that they needed to figure out the discrimination's underlying rule using the feedback provided for each response. The implicit instructions are analogous to the operant methodology used to train songbird subjects on an equivalent task in the next Chapter. Since other species lack the capacity to receive verbal instructions, operant methodology requires that an animal subject recognizes whatever rule underlies auditory discriminations using feedback – typically reinforcement that indicates whether the most recent response was correct/incorrect. Before examining the capacity of other species to learn this task, it was necessary to determine if a rule concerning the presence of a beat could also be learned by human participants without explicit instructions.

2.1.2 Clock-Induction Model of Beat Perception

Several prominent theoretical models of beat perception are described in the literature that each make predictions about processes that contribute to humans' perception of beat. Some

models concentrate on properties of intervals of time, while others approach perception by looking to entrainment of neural oscillations to rhythm (see McAuley, 2010 for a thorough review of various perspectives). Although core differences exist between these models, collectively they have provided a framework for research that has furthered our understanding of the mechanisms implicated in beat perception in humans. From a comparative perspective, it is unknown whether these models can be used to make predictions about perceptual processes in other animals. In this thesis I followed a prominent interval model in creating auditory rhythms for use in human and non-human animal experiments. The latter was intended to explore the applicability of the chosen model to temporal processing in a species of songbird.

Being that rhythm is inherently temporal, models of rhythm and beat overlap with more general models of timing that primarily concern the perception of single intervals (reviewed by Grahn, 2012). Interval timing is well studied in humans and in a variety of other animals. But musical rhythm is too complex for its perception to be wholly explained by these basic timing models: rhythms contain multiple intervals between event onsets that can vary in duration from approximately 0.1 to 2 seconds (Parncutt, 1994; Warren, 1993). Some rhythms may be organized into metrical hierarchies in which a listener may perceive periodicities at multiple levels (Essens, 1986). Consistent perceptual grouping of event onsets is thought to be important for processing meter in speech and music (Frazier et al., 2006; Cooper & Meyer, 1960). By perceptually organizing the events in a rhythm into same-sized groups, a listener may create a higher-level periodicity that spans the onsets of groups.

In this thesis I follow the Povel & Essens clock-induction model to create non-musical auditory stimuli that contain a regular beat. With their model, Povel & Essens (1985) identify temporal features of rhythms that contribute to the perception of accents. An accent occurs when

an event in a sequence is subjectively experienced as more salient than the events that directly precede or follow it. Accents in music may be induced by cues from multiple acoustic qualities, such as periodic changes in the intensity, frequency or harmony of notes (Bigand, 1997; Dawe et al., 1995; Ellis & Jones, 2009). The regularity of a beat can be physically represented in a piece of music in the form of this variation. However, apart from these physical qualities, accents that derive from temporal structure of rhythm are considered the most important for determining meter (Hannon et al., 2004) and listening to music (Drake et al., 2000; Longuet-Higgins & Lee, 1984). Accents may be perceived in simpler rhythms in which physical qualities of sound are held constant and the only features that are made to vary are the durations of inter-onset intervals between events. Povel & Essens label such patterns "equitone" (equal tones).

The Povel & Essens model predicts that induction of a beat depends on the temporal distribution of accents that are perceived in a rhythm. This distribution is determined by a set of rules about the positioning of sound events and silent intervals between them. In general, if an event is relatively isolated in time (not closely followed by other event onsets) then the listener will perceive an accent on that event (Parncutt, 1994). An accent will also fall on the second event within a perceptual grouping of two, and on the first and final event in a grouping of three or more (Povel & Okkerman, 1981). The model states that the brain will encode the temporal distribution of accents relative to an internal clock that is mentally superimposed onto the stimulus. This clock is made up of identical isochronous units (intervals between "ticks" of the clock), whose duration is determined by a process of comparing the fit of multiple possible clock units with the distribution of accents perceived in a given rhythm. The clock unit that is ultimately chosen is whichever best matches the temporal distribution of accents. Listeners that

are exposed to Western music are predisposed to expect future events in rhythm to fit with duple meter (Vuust and Witek, 2014; van der Weij et al., 2017) which coincides with a 4-clock.

In the final stage of matching the "best clock" to a rhythm the listener will calculate the negative evidence, or "counterevidence", against the fit of each possible clock to the accent structure. Counterevidence against a clock is constituted by all the "ticks" of that clock that land on unaccented events or on silent intervals between events. The model predicts that the ease with which a listener may perceive a beat in rhythm is determined by the counterevidence score against the selected clock. Povel & Essens tested the model in a series of experiments and found that participants reproduced rhythms whose ''best clock'' had less negative evidence more accurately than rhythms whose "best clock" had more negative evidence. They also report that participants judged the former to be simpler, whereas rhythms with more counterevidence are described as being higher in complexity (Essens & Povel, 1985; Povel & Essens, 1985).

There are some limitations of this model that are worth noting. The Povel & Essens model only considers the contributions of negative evidence against the selection of a clock and ignores positive evidence – the number of accents that align in time with the "ticks" of the clock. McAuley et al., 1999 tested an opposite version of the model that only considered positive evidence, and found individuals' preferred use of positive or negative evidence for finding a beat was related to their musical training in that musicians were less affected by negative evidence than nonmusicians. (McAuley, 1999). Secondly, the model favors longer clock units (isochronous intervals) since longer units will allow for fewer instances of negative evidence to accumulate as possible clocks are matched with accent structure (Povel & Essens, 1985). Lastly, the Povel & Essens model, as well as other clock models, do not account for the fact that the

structure of accents may be influenced by repetition of a rhythm, which has been shown to affect perception of metrical structure (Temperley & Bartlette, 2002).

Some research has examined whether the presence of low integer ratio relationships between interval durations in a rhythm predicts perception of a beat (e.g., Sakai et al., 1999). However, when accent structure is accounted for, the presence of integer ratio relationships does not necessarily improve performance on beat-based tasks (Grahn & Brett, 2007). Several previous studies on rhythm perception (e.g., Grahn & Brett, 2007; Grahn & Rowe, 2009; Cameron & Grahn, 2014; Bouwer et al., 2018) have divided sequences of intervals that share whole integer-ratio relationships into two types: metric simple (MS) and metric complex (MC). The experiments described in this chapter test whether humans can learn a categorical discrimination between MS and MC equitone patterns. Integer notation is used to indicate the durations of inter-onset intervals in the patterns, with 1 representing the shortest base interval and larger integers (2, 3, 4) representing multiples of the shortest interval.

In metric simple patterns, a tone always occurs on each metrical beat position, and so the periodic onsets of perceptual groups will align consistently in time with accented events. The Povel & Essens model predicts that metric simple patterns will induce a beat with a period that is comparable with the unit of the selected clock. In metric complex patterns, due to the temporal arrangement of events, consistent perceptual grouping is not possible. Metric complex patterns do not have tones at all metrical beat positions, and therefore lack the higher-level periodicity that is created by perceptual grouping of events in metric simple patterns. Accents that are perceived in metric complex patterns will be more irregular and do not align in time consistently with a clock. The model predicts that a listener will therefore experience difficulty in finding a regular beat in complex patterns. In terms of counterevidence, metric simple patterns have little

to no negative evidence against the selected clock, whereas metric complex patterns have relatively more negative evidence (Figure 2.1).

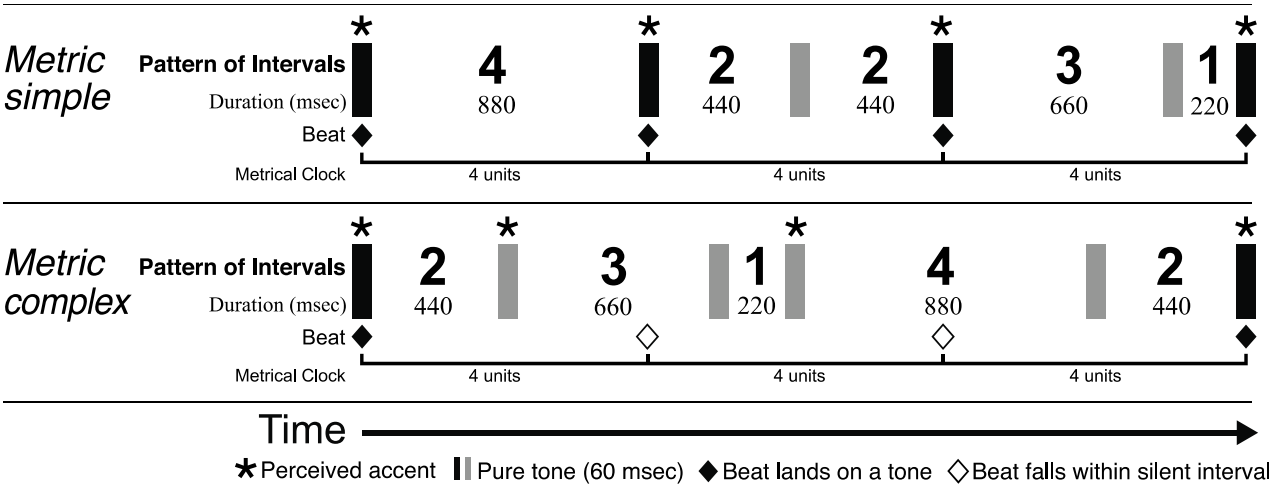

Figure 2.1. Schematic of two equitone patterns identifying their temporal structure in terms of the Povel & Essens model. Integers represent the relative duration of inter-onset intervals. Filled bars represent the position of tones: black are accented tones that align with a regular beat (the units of the metrical clock) and grey are other tones in the rhythm that do not align. Asterisks indicate where accents should be perceived (Povel & Okkerman, 1981). In the metric simple, accents occur at regular intervals that align consistently with the metrical clock. In the metric complex, accents occur at irregular intervals, and do not fit the metrical clock.

The brain's encoding of metrical structure has also been studied using nonmetric rhythms, which contain intervals that share non-integer ratio relationships. Grahn & Brett (2007) found that discrimination performance was similar for metric complex and non-metric rhythms. In some temporal reproduction studies, a subset of subjects distorted non-integer ratios into integer ratios in their tapping of nonmetric sequences (Collier & Wright, 1995; Essens, 1986; Essens & Povel, 1985). One important characteristic of nonmetric rhythms is that they contain intervals durations that do not neatly fit an integer ratio, and consequently metric and nonmetric

rhythms cannot share all of the same intervals. For the experiments described here, it was important that subjects could not use some task-irrelevant feature to discriminate auditory patterns, such as attending to a specific interval duration unique to only one of the stimulus categories. I therefore excluded non-metric patterns and used only metric simple and metric complex patterns that shared common intervals.

2.1.3 The Role of Musical Expertise in Beat Perception Ability

Universal though it may be, humans vary widely in their ability to extract a beat from musical rhythm (Grahn & McAuley, 2009). Individual differences in beat perception ability may be explained, in part, by past experiences with music. A positive relationship is thought to exist between an individual's musical expertise and their beat perception and production ability. It is intuitive that prolonged exposure to music would increase sensitivity to the regularities present in music (van der Weij et al., 2017; Vuust & Witek, 2014). Numerous investigations have considered effects of prior musical training on perception and production of beat (Cameron & Grahn, 2014; Geiser et al., 2010; Grahn & Rowe, 2009; Vuust et al., 2005). These studies have found evidence to suggest that musicians bear an advantage in detecting and keeping a steady beat. In this Chapter I compare performance on a beat perception task across levels of musical expertise by obtaining demographic information from participants about their musical training and skill.

2.1.4 Chapter Overview

I tested human participants in two experiments in which they learned to discriminate between metric simple (MS) and metric complex (MC) equitone patterns. The experiments differed only in the instructions that were provided, so as to manipulate the participants' awareness of a beat in the stimuli. In other behavioural tasks, the strength of a beat perceived in

similar auditory rhythms has been measured using a rating scale (Henry et al., 2017) but here the simple and complex patterns were discriminated on a categorical basis, with the categories framed differently in the two experiments. The influence of individuals' musical expertise on their discrimination accuracy was examined. Performance on this task was compared with scores on a separate test battery that measures beat perception and production ability, the Beat Alignment Test. This discrimination task may be adapted to test beat perception in other animals, as discussed in the other chapters, but here I set out to determine that it can also be learned by humans.

2.2 Methods

2.2.1 Task Summary

The explicit and implicit experiments each included three phases: training, transfer and testing. Human participants were to learn to discriminate a random subset of stimuli during a training task, which consisted of three blocks of trials in which the same stimuli were each presented twice in randomized order. Following training they would next extend the learned rule to novel stimuli in a generalization task, which encompassed both the transfer and testing phases. The transfer phase maintained the subject on the discrimination rule learned in the training by repeating a subset of the stimuli on multiple trials, while the testing phase involved generalizing the rule to novel stimuli. The ability of the participants to learn this discrimination is thus indexed by their accuracy on the generalization task, but I also examined individual differences in performance within the training task. These experiments were designed to approximately match an operant procedure used to test songbirds on the same discrimination in Chapter 3. However, a key difference between the human and non-human animal experiments was that the tested human participants did not need to meet any kind of performance threshold in order to

advance through the experiment, while the songbirds may require multiple sessions of repetitive trials in order to achieve an accuracy criterion and to progress past the training.

2.2.2 Explicit and Implicit Instructions

Prior to the experimental sessions participants were pseudorandomly assigned to one of two experiments, labelled explicit and implicit. The experiments differed only in the semantic content of instructions delivered to participants at the beginning of the session. Within the explicit instructions, participants were provided with a definition of the beat as a regular pulse experienced while listening to music, an overt explanation of the task and information about the "stronger beat" and "weaker beat" response options. In the implicit instructions, participants were only taught how to select between the two response options; they were told that the sounds in each of the two categories all had something in common and that they needed to figure out the rule underlying the discrimination using the provided feedback. For full scripts of the instructions used in both the explicit and implicit experiments see Appendix Tables 1 and 2.

At the start of the session, participants were first administered verbal instructions by the experimenter. Secondary redundant instructions were displayed on-screen and were repeated at the start of each of three consecutive blocks of training trials. The instructions were followed by presentations of two exemplar metric simple (42231, 112422) and metric complex (214311, 141321) patterns in alternating order and participants were prompted to sort them into the first and second category respectively on four practice trials. These patterns were not repeated as stimuli during the experiment. Participants were free to ask for clarification from the experimenter during training; in response to questions the experimenter would repeat relevant portions of the instructions.

Importantly, in both the explicit and implicit instructions, participants were told twice – once verbally by the experimenter and again in the on-screen instructions – to remain as still as possible for the duration of the experiment and to refrain from any kind of body movement during the task. Since these experiments concerned only beat perception and not production, this instruction to refrain from movement was intended to discourage participants from tapping along to the rhythms. If the participant was observed moving along to the sounds the experimenter would remind them to refrain.

2.2.3 Subjects

Seventy-seven undergraduate students participated from the Psychology Research Participation Pool at The University of Western Ontario (49 female, 28 male; average age 18.6 years). Thirty-nine participants were selected to complete the explicit instructions experiment, and thirty-eight participants completed the implicit instructions experiment. Participants were compensated with course credit. All participants completed a pre-screen survey. Individuals who had previously participated in other studies of beat perception were excluded, and all were screened for normal hearing. To recruit individuals with musical expertise, a criterion was applied such that only those who reported 5 or more years of experience playing a musical instrument were qualified as eligible to participate. This criterion was lifted for recruiting non-experts.

2.2.4 Materials

2.2.4.1 Auditory Rhythms

The metric simple and complex auditory rhythms used as stimuli in these experiments were generated in Matlab 2017b. All were constructed of identical 1500 Hertz pure tones that were 60

ms long with 10 ms on/off ramps. The stimuli all shared the same overall duration of approximately seven seconds. The base interval (smallest possible temporal unit) that was used in the stimuli was 1 = 220 ms, and each metrical pattern contained only the following interval durations in various combinations: 220, 440, 660, 880 ms (denoted as 1-4 respectively). Humans may perceive a beat in rhythms within a limited range of tempi – approximately 100-120 beats per minute (McAuley et al., 2012). The rate of these stimuli was selected so as to fall within this range while maintaining compatibility with the perceptual sensitivities of the tested songbird species. Stimulus design considerations for the latter are discussed further in Chapter 3.

In many lines of rhythm research, including comparative studies with other species, auditory stimuli are presented repetitively by concatenating iterations of a rhythm together. One benefit of these looping presentations is that they provide longer exposure to each stimulus and a greater chance that the listener will perceive regularity. But looping repetitions may make the boundaries of a pattern ambiguous. For instance, consider the patterns 22413 and 32241, both used as stimuli in this study. These two patterns contain the same relative ordering of intervals and can be described as phase-shifted (by moving the final 3 of the first pattern to the first interval of the second pattern). When these acoustic stimuli are each presented once, it is perceptually obvious (to humans) that they are distinct from one another, but when looped, the beginning and end of the patterns are made ambiguous and they may become indistinguishable. Single presentations of a stimulus do not have this ambiguity; however, a single presentation may be too short to induce a beat, and so multiple presentations are needed.

To ensure enough exposure to induce a beat, but to avoid boundary ambiguity due to looping, the acoustic stimuli in these experiments repeated a rhythmic pattern only twice and separated the two iterations of the pattern by a consistent, relatively long (1.8 s) silent duration,

which pilot testing indicated was long enough for the iterations to be perceived as separate. The longest inter-onset interval used in any of the patterns was 0.880 s, so 1.8 s was not confusable with a particularly long interval within a pattern. Many previous experiments have used similar auditory rhythms to test beat perception, but with presentations that are longer and involve multiple serial repetitions of a pattern. Pilot testing results indicated that just one repetition of a pattern within each stimulus was sufficient for human participants to correctly categorize the stimulus as "stronger beat" or "weaker beat". In these experiments I sought to examine how these shorter rhythm presentations are perceived with respect to a discrimination based on beat strength. For our testing purposes, shorter stimulus presentations allowed for a greater number of trials to be performed in a single experimental session. I also considered that providing many repetitions of patterns would make it easier for the subject to detect regularity, which may in turn increase their likelihood of responding "stronger beat" to metric complex stimuli.

2.2.4.2 Stimulus Categories

A total of 44 unique equitone stimuli were generated by permuting ten parent sets of 5-7 intervals that were mostly obtained from Grahn & Brett, 2007 (Table 2.1). The patterns were split into two categories based on their counterevidence scores against a metrical 4-clock. The temporal composition of the stimuli was carefully selected so that there was no way for the patterns to be discriminated (yielding above-chance performance) without the subject detecting the regularity of periodic temporal accents and using this as a categorical rule. All distinguishable properties of the two stimulus categories were balanced such that no feature was common in one category but not the other. The representation of each parent set of intervals, the total number of intervals in the pattern, the first interval in the pattern, the final interval in the pattern, the inclusion of runs of identical intervals (i.e., 111) or combinations of intervals (i.e., 21

or 212) were made as consistent as possible between the two categories, though for some of these features the balance was more exact than for others. For a breakdown of the distribution of these elements across the two categories please see Appendix Tables 3 and 4.

Table 2.1. The full pool of 44 equitone stimuli used in the explicit and implicit experiments, as well as in the first operant experiment described in Chapter 3. The stimuli are split into two categories: metric simple (MS) and metric complex (MC), depending on their computed counterevidence score against a 4-clock in keeping with the Povel & Essens model. The intervals in these patterns are represented with sequences of integers (1-4). An integer value denotes the relative length of an inter-onset interval. Each duration is a multiple of 220 milliseconds.

Category 1: Metric Simple "Stronger Beat"				Category 2: Metric Complex "Weaker Beat"			
Stimulus Pattern	Parent Interval Set	Number of intervals	Counterevidence (against 4-clock)	Stimulus Pattern	Parent Interval Set	Number of intervals	Counterevidence (against 4-clock)
22224	22224	5	0	12432	12234	5	9
41331	11334		1	14133			9
22314	12234		0	14232			9
22413			1	23142			8
31224			0	23241			8
31422			0	32241			8
221331	112233	6	1	231132	112233	6	8
311322			1	331221			8
112314	111234		0	321114	111234		4
411231			0	141123			9
411222	112224		0	122241	112224		9
211422			0	412212			5
422112			0	142212			9
1123122	1112223	7	0	212241			8
3122112			0	1111143	1112223	7	6
4221111	1111224		0	1211232	1111224		5
2211114			0	1221114			5
1122114			0	1314111	1111233		4
3131112	1111233		1	1411311	1111134		9
3141111	1111134		0	2411121			5
4111131			0	3114111			5
1111431			0	3121311			6

2.2.4.3 Randomization of Stimulus Presentations

For each participant the full pool of stimuli was divided into three subsets: 12 stimuli in a training subset, 8 stimuli in a transfer subset and 24 stimuli in a testing subset, each with an equal number of metric simple and metric complex stimuli. These subsets corresponded to presentations in the three phases of the experiment. For randomizing the allocation of patterns to the subsets, I produced 30 unique randomizations of the order of a list of all 44 stimuli. The randomizations were split at consistent points into the three subsets. I then assigned each randomization to subject numbers within both of the experiments so that only 1-2 individuals would experience each randomization. The stimuli presented in the training, transfer, and testing phases were thus different for each participant.

2.2.4.4 Testing Setup

The participant sat at a desk in front of a laptop computer inside a quiet room. Acoustic stimuli were presented through Sennheiser HD280 Pro headphones connected to a laptop computer through an external sound card (UR22mkII Steinberg USB audio interface). The presentation volume was pre-set at 65 dB, though the participant was allowed to adjust this to a comfortable setting. The experiments were coded and executed in E Prime 2. The behavioural data were processed in Matlab 2017b and Microsoft Excel, and statistics were computed in SPSS Statistics and JASP.

2.2.5 Pilot Testing

I conducted pilot testing with 30 human participants to refine the metrical stimulus categories. The pilot participants performed a discrimination of 60 unique metric simple and metric patterns that were each presented three times. They were instructed to categorize each

stimulus as “stronger beat” or “weaker beat”. The presentation order of stimuli was randomized and feedback (correct/incorrect) was provided for each response. An analysis of participants’ average discrimination accuracy for each stimulus identified sixteen patterns that were especially prone to being misclassified, so these were eliminated from the final set.

2.2.6 Experimental Procedure

2.2.6.1 Trial Procedure

The participant initiated trials by pressing the spacebar key on the laptop. A trial would begin with the message “Listen to this sound” displayed onscreen, accompanied by the auditory stimulus. Responses were not permitted during stimulus presentations. After the sound ended, participants were prompted on-screen to respond by pressing either the 1 or 9 keys on the keyboard, which were labelled with colored stickers. In the explicit instructions experiment, this prompt would ask if the most recently presented stimulus had a “stronger beat” (press 1) or “weaker beat” (press 9); in the implicit instructions experiment the prompt would simply ask which category the stimulus belonged to (press 1 or 9).

2.2.6.2 Trial Feedback

For the training task, as well as the transfer trials of the generalization task, all responses were immediately followed by trial feedback which consisted of the words “correct” or “incorrect” appearing briefly on-screen. In addition to this feedback, each correct response would earn one point added to a cumulative counter shown in the bottom corner of the display. Participants were instructed to earn as many points as they could and were told the maximum possible points they could receive in the experiment. The points counter was implemented for equivalence with the comparative operant experiment discussed in Chapter 3, in which a tangible

food reward was provided on correct trials. I added this secondary form of feedback so that participants could use it to objectively track their overall performance across trials. The participant's balance of accrued points was reset between the training and generalization tasks.

2.2.7 Training Task

The training task contained 72 trials divided into three blocks of 24 trials. Within each training block, 12 randomly-selected stimuli (6 MS and 6 MC) from the training subset were presented twice, with the same stimuli reoccurring in all three blocks. The order of stimulus presentations was randomized within each block. Each response was accompanied by trial feedback.

At the end of each block a message was displayed on-screen rating overall performance on the most recent 24 trials: for accuracy of greater than 80 percent of trials correct, a ranking of "expert" was given; for 60 to 79 percent correct the ranking was "intermediate" and for less than 60 percent correct the ranking was "novice". This block feedback was included to provide the participant with an indication of the effectiveness of their most recently applied discrimination strategy during training, which was particularly important for participants that were implicitly instructed and whose initial strategy may have been irrelevant to the task. Between the training blocks, the on-screen instructions displayed at the beginning of the experiment would repeat with additional presentations of the category exemplar patterns.

Due to a programming error, if a ranking of "novice" was received on the third block of the training, no block feedback was provided, and the experiment would instead proceed directly into the instructions for the generalization task. This affected only 7 individuals that ranked "novice" on the third block of training prior to the program error being fixed. A comparison between these participants and others found performance was not significantly affected.

2.2.8 Generalization Task

The generalization task directly followed the training and consisted of 120 trials. This task contained two phases in the form of distinct trial types labelled as transfer and testing. The transfer phase included 8 stimuli from the transfer subset that were each presented on 12 trials throughout the task. The testing phase contained 24 stimuli from the testing subset that were each presented only once to each participant. On transfer trials all responses were accompanied by trial feedback, while on testing trials no feedback was provided, and the response would lead directly into the next trial. As in the training, within the generalization task the presentation order of stimuli was randomized (within the subsets), and the sequential order of transfer and test probe trials was randomized for each individual. The on-screen instructions that preceded the generalization task included a repetition of the earlier instructions for responding on the keyboard and warned the participant that they would be hearing new rhythms and that some trials would not provide feedback.

The distinction between transfer and testing phases was equivalent to the procedure used in the comparative operant experiment discussed in Chapter 3. It was important to ensure that the non-human animal subjects were motivated to continue responding throughout testing sessions. One method is to use a variable reinforcement schedule, such that on a designated proportion of trials (in this case, 20 percent) the subject's response will not produce any feedback. In both the comparative operant experiment and the generalization task of the present experiment, transfer trials occurred more frequently ($P = 0.80$) and involved multiple presentations of a subset of 8 stimuli, always followed by response feedback. The testing trials ($P = 0.20$) lacked response feedback and each of the 24 stimuli in the testing subset was presented only once. Though both the transfer and testing trials were included in analyses, the testing stimuli were used to probe

generalization from the training task to novel patterns, while the transfer trials were meant to maintain the subjects on the discrimination rule previously learned in the training with other stimuli. To account for differences between the transfer and testing phases in the number of presentations of each stimulus and in the provision of feedback, accuracy scores for transfer and testing were calculated separately.

2.2.9 Debrief Questionnaire

After the participant completed the generalization task, a debrief questionnaire was immediately administered. The debrief questionnaire captured relevant demographic information about each individual, as well as their reports of any strategies they used during the experiment. Several items included in the questionnaire pertained to the participant's previous musical experience and skill (Appendix Table 5). The participants' responses to some items are discussed with the results of this experiment, and their reported strategies are discussed further in Chapter 4.

2.3 Beat Alignment Test (BAT) Production & Perception

Administration of the debrief questionnaire was followed by the Beat Alignment Test (BAT) (Müllensiefen et al., 2012) which was used to assess participants' ability to detect and synchronize their movement to a regular pulse in music (Iversen & Patel, 2008). The BAT includes two subtests: a production task and a perception task.

2.3.1 Materials

Both subtests of the BAT use the same 17 clips of Western music from different musical genres (rock, pop, jazz and orchestral), enabling direct comparisons between perception and production scores. The order of stimulus presentation was random for each individual.

2.3.2 Procedure

In the perception task, participants listened to musical stimuli with superimposed isochronously-spaced auditory beeps and indicated whether the beeps were on or off the beat of the music. Scores on the perception task were calculated by taking the proportion of trials that a participant responded correctly as "on" or "off" the beat. In the production task, participants tapped in synchrony to the beat on the spacebar key while listening to musical stimuli. Before each task, the participant practiced a single trial to familiarize them with the procedure. The production and perception task together lasted approximately 10 minutes.

Analysis of production response data yielded three scores that measure the accuracy and variability of the participant's tap times relative to the stimulus: the coefficient of deviation (CDEV), the asynchrony score (ASYNC) and the coefficient of variation (CoV). The CDEV is the absolute difference between the duration between each tap (inter-tap-interval, ITI) minus the duration between each beat in the stimulus (inter-beat-interval, IBI) divided by the mean ITI (equation 2.1). The IBI is selected as the closest in time to the nearest ITI. CDEV measures how accurately the tap rate matches the beat rate (tempo) but does not take into account whether the participant's taps were aligned in time with the beat. More accurate tempo matching will produce lower CDEV scores, while less accurate tempo matching will result in higher CDEV scores.

$$\text{CDEV} = \frac{|\text{ITI} - \text{IBI}|}{\text{mean ITI}}$$

Equation 2.1. Calculation of the coefficient of deviation for the BAT production subtest.

The ASYNC score measures the absolute difference between the participant's tap times and the nearest corresponding beat times over the entire stimulus. These absolute differences are then averaged together and divided by the average ITI. Lower asynchrony scores indicate better

synchronization than higher scores. The CoV is a measure of variability in the regular timing of a participant's taps, irrespective of the stimulus; lower CoV indicates less variability between the ITIs within trials. CoV is calculated by dividing the standard deviation of ITI by the average ITI.

In summary, the experiments were completed in this order: training, generalization, questionnaire, BAT production task and BAT perception task. Participants were permitted to take short breaks at any point. The experiments lasted approximately 50 minutes. At the end of the session the participants were debriefed and a full explanation of the experiment was provided.

2.4 Results and Statistical Analyses

2.4.1 Capturing Beat Expertise

Between the questionnaire and BAT, a total of seven variables captured some aspect of the participant's musical expertise: three questionnaire items (a 1-10 self-rating of their overall musical skill, a 1-10 self-rating of their ability to detect the beat in music, and the number of years they had received musical training) and four scores obtained from the BAT (CoV, ASYNC, CDEV and perception score). A factor analysis revealed some of these variables to be significantly intercorrelated (Table 2.2). Within the BAT, only the production CoV and the perception score were significantly correlated with discrimination performance and with each other. The ASYNC and CDEV scores did not significantly predict the other variables or accuracy on the generalization or training tasks and were therefore excluded in the analyses.

The relationships between factors were consistent across individuals. Participants who scored highly on the BAT and who reported on the debrief questionnaire that they had more years of musical training and a high self-rating of musical skill performed better on the discrimination than participants who performed poorly on the BAT and reported less musical

experience. There were moderate correlations between discrimination accuracy on the generalization task and two scores from the BAT (CoV and perception scores) and between the generalization task and the three questionnaire items. Three participants failed to complete the BAT or left blank the items of interest on the questionnaire, so scores from these individuals were excluded from comparisons.

Table 2.2. Correlation matrix of five variables that captured musical expertise, including three items from the debrief questionnaire and two scores from the Beat Alignment Test (BAT), as well as accuracy within the training and generalization tasks averaged across participants. Values indicate Pearson correlations and significance for a 2-tailed test. Italics mark the comparisons which do not meet the threshold for significance under a False Discovery Rate correction.

	Generalization Accuracy	Training Accuracy	Years of Musical Training	Self-Rating Beat Ability	Self-Rating Musical Skill	BAT CoV	BAT Perception Score
Generalization Accuracy		.622**	.337**	.274*	.385**	-.407**	.302**
		.000	.003	.017	.001	.000	.009
Training Accuracy	.622**		.409**	*.215*	.489**	-.324**	.240*
	.000		.000	*.064*	.000	.005	.039
Years of Musical Training	.337**	.409**		.354**	.638**	-.494**	.313**
	.003	.000		.002	.000	.000	.007
Self-Rating Beat Ability	.274*	*.215*	.354**		.583**	-.315**	.401**
	.017	*.064*	.002		.000	.007	.000
Self-Rating Musical Skill	.385**	.489**	.638**	.583**		-.414**	.265*
	.001	.000	.000	.000		.000	.022
BAT CoV	-.407**	-.324**	-.494**	-.315**	-.414**		-.403**
	.000	.005	.000	.007	.000		.000
BAT Perception Score	.302**	.240*	.313**	.401**	.265*	-.403**	
	.009	.039	.007	.000	.022	.000	

2.4.2 Principal Component Analysis

As the multiple measures of musical expertise were significantly intercorrelated, I performed a principal components analysis to extract orthogonal factors. A single index variable

labelled Beat Expertise was produced and included in two analyses of variance of discrimination accuracy.

Table 2.3. Factor analysis values for demographic questionnaire items and BAT scores that capture musical expertise. These variables clustered into a single principal component labelled Beat Expertise that was included in other analyses as a between-subjects factor.

	Beat Expertise Loading
Years of Musical Training	0.601
Self-Rating Beat Ability	0.504
Self-Rating Musical Skill	0.655
BAT CoV	0.518
BAT Perception Score	0.389
Eigenvalue	2.668
% of variance	53.4
Cumulative %	53.4

2.4.3 Analysis of Training and Generalization Performance

Accuracy within the three training blocks was averaged across trials for each participant, yielding an individual score for each block. Within the generalization task, accuracy scores were calculated separately across transfer trials and testing trials. Thus, for each participant, accuracy was split into five levels of a repeated measures factor labelled trial bin, with bins 1-3 containing the three blocks of the training phase and bins 4 and 5 containing the transfer and testing phases.

To examine the effect of musical expertise on discrimination performance, I divided participants' ranked scores on Beat Expertise into three bins labelled Novice, Intermediate and Expert. Each bin contained an approximately equal number of participants. In terms of demographic differences between the bins, significant differences were found in the average number of years of musical training in Novice, Intermediate and Expert, $F(2) = 33.35$, $p < .001$. The mean number of years of musical training for participants within each bin were as follows:

Novice, mean = 2.38, SD = 2.08; Intermediate, mean = 5.68, SD = 2.80; Expert, mean = 8.89, SD = 3.31.

I ran a 2 x 5 repeated-measures ANOVA that included Beat Expertise bin and instruction type as between-subject factors, and trial bin as the within-subject factor (Figure 2.2). There was a significant interaction between instruction type and binned Beat Expertise, $F(2, 67) = 3.75$, $p = 0.03$. Simple main effects analysis showed that when provided explicit instructions on the task, experts performed significantly better than novices ($p < 0.001$), but when provided implicit instructions the difference in performance between experts and novices was non-significant overall ($p = 0.08$). The graphs below illustrate the differences between the means of the three Beat Expertise bins across each of the levels of the Trial Bin factor, spanning the training and generalization tasks. Within the explicit instructions, both Intermediate and Expert participants were significantly more accurate than Novices on the second (Intermediate-Novice, $p = 0.008$; Expert-Novice, $p = 0.002$) and third (Intermediate-Novice, $p = 0.003$; Expert-Novice, $p = 0.001$) blocks of the training task. Explicitly instructed Experts were also significantly more accurate than Novices on the transfer ($p = 0.007$) and test probe ($p = 0.006$) trials. Within the implicit instructions, Experts did not significantly outperform Intermediate or Novice participants consistently across the three blocks of training. However, implicitly instructed Experts were significantly more accurate on the transfer trials than Intermediate ($p = 0.011$) or Novice ($p = 0.007$) participants, as well as on the test probe trials (Intermediate, $p = 0.043$; Novice, $p = 0.05$).

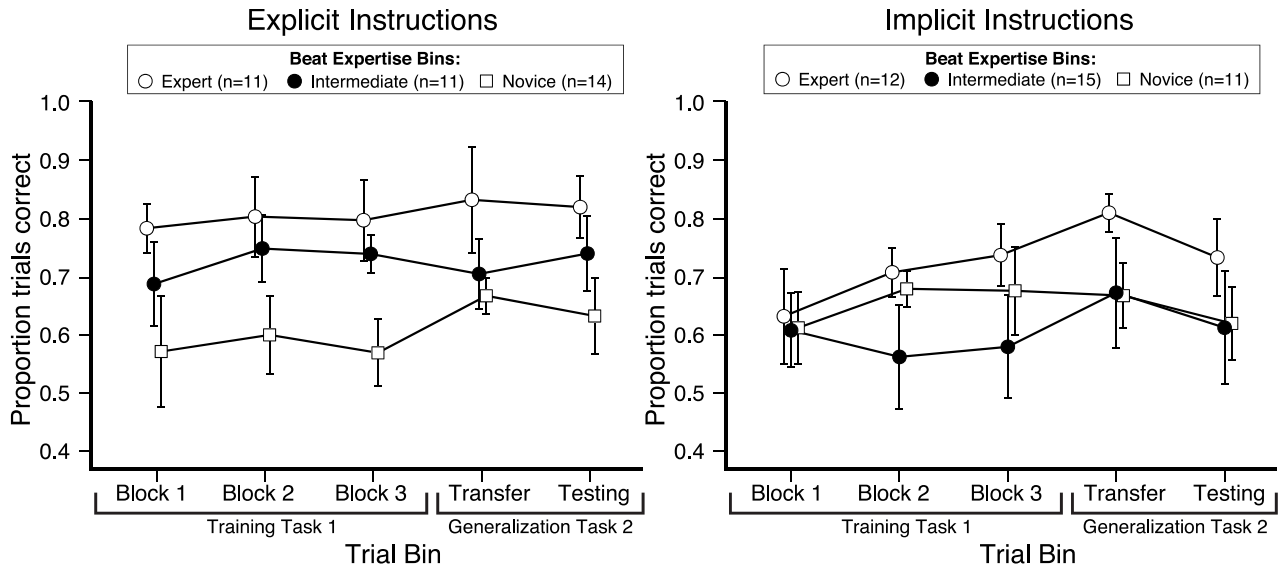

Figure 2.2. Repeated measures ANOVA of discrimination accuracy across the training and generalization tasks. Marked lines show averages within the three bins of Beat Expertise (novice, intermediate, expert). The number of subjects in each bin is indicated above. Accuracy across the explicit/implicit instructions was found to differ significantly and performance within the two experiments is therefore shown separately. Error bars depict a 95% confidence interval.

2.4.4 Effect of Motor Synchronization

All of the participants were instructed twice to refrain from tapping along to the stimuli. However, approximately half of the participants in both of the experiments indicated on the debrief questionnaire that they had moved along to the sounds despite these instructions. Moving along to the stimuli could have potentially improved performance on the MS rhythms and perhaps made it easier to find the beat in some MC rhythms, resulting in them being misclassified. To compare performance of participants who tapped along with those who did not, each individual's movement (did tap vs did not tap) was included as a factor in a second analysis.

I ran a 2 x 2 x 2 repeated measures ANCOVA on participants' accuracy scores to examine whether movement influenced perception of metric simple and metric complex patterns.

For this analysis I excluded scores from the training task and focused solely on the 120 trials of the generalization task, collapsing across the transfer and testing phases. Responses were averaged within the metric simple and metric complex. The analysis included rhythm type (simple/complex) as a within-subject factor and instruction type (explicit/implicit) and movement (did tap/did not tap) as between-subjects factors. Individual scores on Beat Expertise were included as a covariate. The ANCOVA revealed a significant main effect of rhythm type, $F(1) = 6.84$, $p < 0.01$, partial $\eta^2 = 0.091$. The main effects of instruction type and movement were nonsignificant. There were no significant interactions between any of the factors. However, a trend can be observed in Figure 2.3 which shows that participants who received implicit instructions and who did tap during the task responded more accurately to metric simple stimuli than those who did not tap.

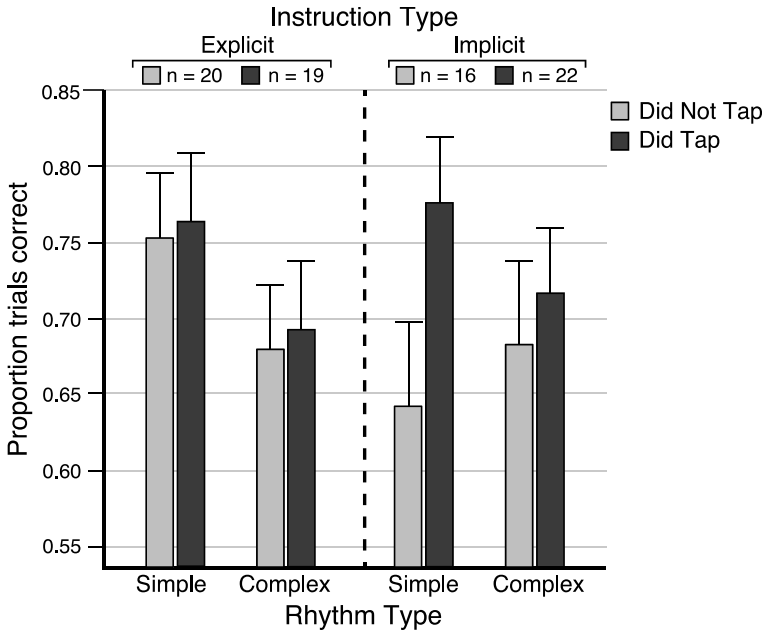

Figure 2.3. Mean discrimination accuracy for the metric simple and metric complex stimuli within the generalization task, including both transfer and testing trials. Data from participants who received explicit and implicit instructions are depicted separately. Light grey bars show responses from participants who indicated on the debrief questionnaire that they did not tap along to the stimuli during the task (as per their instructions). Dark grey bars show responses from participants who did tap along during the task. Error bars show a 95 percent confidence interval.

2.4.5 Sensitivity and Response Bias

I conducted a signal detection analysis to examine whether sensitivity and response bias varied across the explicit/implicit instructions or across Beat Expertise. A correct response to a MS stimulus (stronger beat) was designated a hit trial, and an incorrect response to a MC stimulus (weaker beat, but incorrectly responded as stronger beat) was designated a false alarm trial. A MS pattern that was labelled as weaker beat constituted a miss, and a MC pattern that was labelled as weaker beat was considered a correct rejection. This analysis only included the transfer and testing trials from the generalization task and excluded the training.

The average d' scores and percent trials correct for each stimulus type were as follows. Within the explicit instructions: d' = 1.479, overall percent correct = 72%, MS percent correct = 76%, MC percent correct = 68%. Within the implicit instructions: d' = 1.444, overall percent correct = 71%, MS percent correct = 72%, MC percent correct = 70%. I compared sensitivity and response bias among the three bins of Beat Expertise (novice, intermediate, expert) within the explicit/implicit instructions. For explicit: novice (n = 14), d' = 1.02, c = -0.05; intermediate (n=11), d' = 1.38, c = -0.21; expert (n=11), d' = 2.34, c = 0.12. For implicit: novice (n=11), d' = 1.10, c = -0.07; intermediate (n=15), d' = 1.18, c = 0.04; expert (n=12), d' = 2.09, c = -0.33. An

ANOVA of sensitivity scores revealed a significant effect of Beat Expertise bin, $F(2) = 3.55$, $p < 0.05$, partial $\eta^2 = 0.10$. Post-hoc comparisons indicated experts were significantly more sensitive than the novices, $t = 2.52$, $p < 0.05$. There were no significant differences in sensitivity or response bias found between instruction types, and bias did not differ significantly between Beat Expertise bins. However, there were wide individual differences between participants in both sensitivity (d' min = -0.36, max = 9.48) and decision criterion (bias) (c min = -3.08, max = 2.91). The variation in these scores may be explained in part by individuals' use of discrimination strategies, which is reviewed in the fourth chapter.

2.4.6 Comparing Performance with Counterevidence Scores

The Povel & Essens model postulates that during presentation of a rhythm, the listener will compile negative evidence against the fit of possible clocks to that rhythm and will ultimately select a clock based on having the least amount of negative evidence (thus fitting the best). This evidence may be indexed with a counterevidence score, which is computed by measuring the fit of a clock to a repeated, looping presentation of a rhythm. In these experiments the stimuli were non-repetitive, featuring only two non-looping presentations of each pattern of 5-7 intervals. To examine whether counterevidence predicts the likelihood of participants detecting a beat in this configuration, the average proportion of correct trials for each metric complex pattern is plotted in Figure 2.4 and ordered by decreasing counterevidence scores against a 4-clock. The metric simple rhythms are excluded here since they contained little to no negative evidence. Discrimination accuracy across the metric complex stimuli was significantly correlated with counterevidence scores in both the explicit experiment, $r(20) = 0.854$, $p < 0.001$, and in the implicit experiment, $r(20) = 0.579$, $p = 0.005$. A two-tailed test of the difference between these correlations was marginally nonsignificant, $Z = 1.88$, $p = 0.06$.

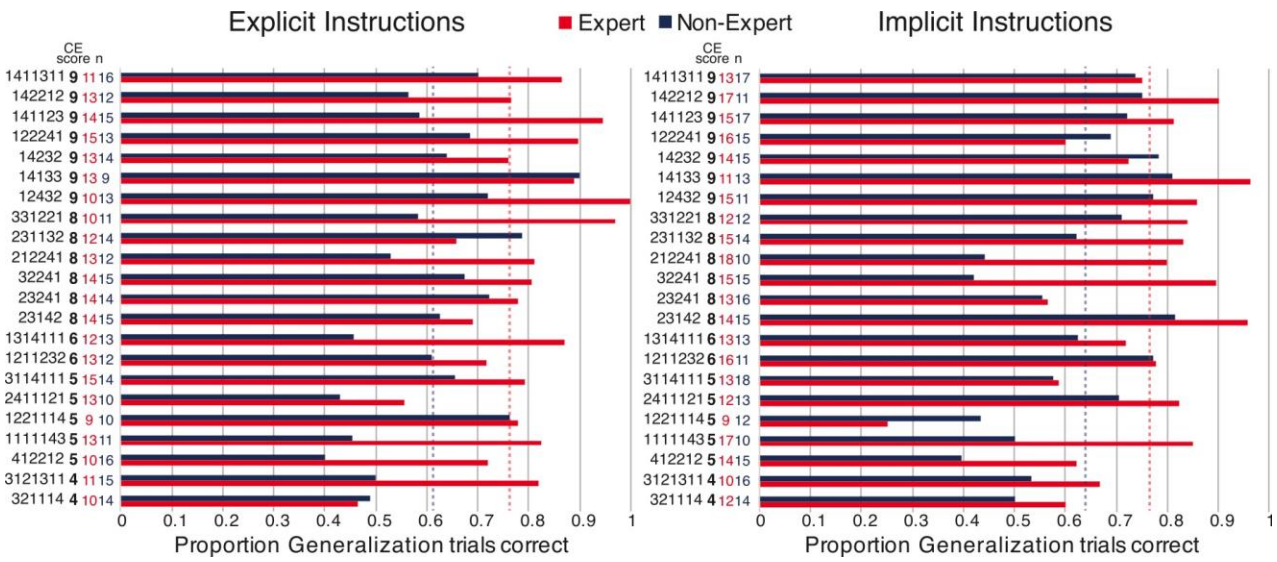

Figure 2.4. Mean discrimination accuracy averaged across participants for each individual metric complex stimulus. The graphs depict differences in accuracy of responding to rhythms with varying amounts of counterevidence (CE) against the fit of a metrical clock. These graphs illustrate that the counterevidence (CE) score predicts accuracy of responding towards the metric complex stimuli. Rhythms are ordered on the vertical axis by decreasing counterevidence (CE) scores. The data are divided into averages within Expert and Non-Expert groups; participants were split at the median of scores on Beat Expertise (shown in red/blue), allowing for comparisons between these groups at the level of individual stimuli. Depicted means only include trials from the generalization task and exclude training. Grand averages across stimuli within expert/non-expert are shown with dotted lines. The number of participants (n) within expert/non-expert groups that contributed to means for each stimulus is shown on the left; differences between these numbers are due to the randomized allocation of stimuli that were presented in the generalization task.

2.5 Discussion

In this chapter I have produced evidence that the applied discrimination paradigm effectively tests humans' beat perception ability. This study is one of many that have used metric simple and metric complex stimuli to probe beat perception in humans, but it is unique in using a metric categorization procedure that can be adapted to test animal subjects and facilitate comparisons across species. With this paradigm the specificity of clock-based temporal processing to humans may be examined in future animal studies. Before it can be used for comparative purposes, it was necessary to first test the paradigm with humans. In the implicit experiment I examined whether the discrimination between simple and complex could be learned by humans without receiving clear instructions. The strong performance of some participants in this experiment suggest that humans can be made implicitly aware of regularity in the accent structure of auditory rhythms even without prior expectations of a beat. It is arguable that the explicit/implicit instructions experiments engaged the distinct top-down and bottom-up attentional systems characterized in previous rhythm investigations (Rohenkohl et al., 2011).

Participants responded significantly more accurately to the simple patterns than they did to complex patterns. Figure 2.3 shows this difference is greater in the implicit instructions group. I offer two possible interpretations of this effect: one based on the behaviour of participants, and a second based on the Povel & Essens model. Response accuracy in the generalization task was highly variable across participants in both the explicit and implicit experiments. The observed low accuracy scores of some of the implicitly-instructed participants (8 individuals scored less than 60 percent of trials correct on the generalization task) suggests that these individuals never figured out the rule underlying the discrimination between simple and complex. But for the participants that did figure out the task, once they started attending to the presence of regular

temporal accents, they may have become biased to find regularity where it was not actually present. Even though they were instructed against doing so, more than half of the participants indicated they moved along to the sounds. This information alone says nothing about whether this movement was synchronized to a beat, nor the accuracy of this synchronization, but entrainment of movement is likely to impact finding of an auditory beat (Su & Pöppel, 2012). If the participants began tapping at the rate of a 4-clock for every stimulus, this may have contributed to perceiving regularity in the metric complex patterns, and would have biased participants to find a beat. The participants' use of cognitive strategies during the task, measured through self-reporting on the debrief questionnaire, is discussed further in Chapter 4.

It may also be the case that reduced accuracy in responding to metric complex stimuli can be explained by participants finding a beat in some of them. The metric complex stimuli were not all of equal complexity. In terms of the Povel & Essens clock-induction model, some of the patterns were more compatible with a 4-clock than others, even though all of the complex patterns had at least some negative evidence against that clock. Computed counterevidence scores for the complex patterns were found to be positively correlated with the proportion of participants' responses that correctly labelled the stimulus as complex. If a complex pattern had a relatively small amount of negative evidence against the fit of a 4-clock, participants were less accurate in labelling it as complex (or "weaker beat" as in the explicit experiment). These findings are thus consistent with seminal work by Povel & Essens on which the applied model is based. They also show that the Povel & Essens model predicts the perception of accent structure even in non-looping presentations of rhythms. Interestingly, accuracy of responding to some stimuli appears to be modulated by participants' musical expertise, as indicated by differences between blue and red bars in Figure 2.4. However, a greater sample size would be needed to

further tease apart the responses by experts at non-experts at the level of individual patterns.

I compared discrimination performance with scores on the Beat Alignment Test in order to validate that the task accesses the capacity of humans to perceive a beat. I factored scores on the BAT into an overall index of participants' Beat Expertise that also included three other quantitative measures of musical skill. I found that discrimination accuracy was significantly correlated with scores on the BAT and that there was a significant simple main effect of Beat Expertise wherein Experts outperformed Novices in both the explicit and implicit instruction experiments. These results support that performance of this task is predicted by individuals' past experience with music and their overall musical skill, including beat perception and variability in beat production. The significant interaction between instruction type and the binned Beat Expertise suggests that scores on Beat Expertise predicted performance differently between the explicit and implicit instructions, but the direction of this difference was unclear from the analysis of variance.

2.6 Chapter Summary

In this Chapter I applied a novel behavioural paradigm to test beat perception in human participants. Accuracy on a discrimination task between metric simple and complex patterns was significantly predicted by individuals' musical expertise. The results of the two experiments demonstrate that this beat-based discrimination can be learned by humans even implicitly, without prior expectations of finding a beat. There were significant differences between discrimination performance in the explicit and implicit instruction experiments, and performance was highly variable across subjects. Even so, averages of accuracy scores reveal that that some participants in both experiments, at least half, were able to learn the discrimination. This finding of successful implicit learning of the task has important implications for applications of this

paradigm to test non-human animal subjects which cannot be explicitly instructed. In the next Chapter I review an operant version of this paradigm for probing the sensitivity of songbirds to beat.

Chapter 2 References

Bigand, E. (1997). Perceiving musical stability: the effect of tonal structure, rhythm, and musical expertise. Journal of Experimental Psychology: Human Perception and Performance *23*, 808–822.

Bouwer, F.L., Burgoyne, J.A., Odijk, D., Honing, H., Grahn, J.A. (2018). What makes a rhythm complex? The influence of musical training and accent type on beat perception. PLoS One *13*, e0190322.

Cameron, D.J., Grahn, J.A. (2014). Enhanced timing abilities in percussionists generalize to rhythms without a musical beat. Frontiers in Human Neuroscience *8*, 1003.

Collier, G.L., Wright, C.E. (1995). Temporal rescaling of simple and complex ratios in rhythmic tapping. Journal of Experimental Psychology: Human Perception and Performance *21*, 602–627.

Cook, P., Rouse, A., Wilson, M., Reichmuth, C. (2013). A California sea lion (*Zalophus californianus*) can keep the beat: motor entrainment to rhythmic auditory stimuli in a non vocal mimic. Journal of Comparative Psychology *127*, 412–427.

Cooper, G.W., Meyer, L.B. (1963). The Rhythmic Structure of Music. Chicago: The University of Chicago Press.

Coull, J., Nobre, A. (2008). Dissociating explicit timing from temporal expectation with fMRI. Current Opinion in Neurobiology *18*, 137–144.

Dawe, L.A., Platt, J.R., Racine, R.J. (1995). Rhythm perception and differences in accent weights for musicians and nonmusicians. Perception & Psychophysics *57*, 905–914.

Drake, C., Jones, M. R., Baruch, C. (2000). The development of rhythmic attending in auditory sequences: attunement, referent period, focal attending. Cognition, 77(3), 251-288.

Ellis, R.J., Jones, M.R. (2009). The role of accent salience and joint accent structure in meter perception. Journal of Experimental Psychology: Human Perception and Performance *35*, 264–280.

Essens, P.J. (1986). Hierarchical organization of temporal patterns. Perception & Psychophysics *40*, 69–73.

Essens, P.J., Povel, D.J. (1985). Metrical and nonmetrical representations of temporal patterns. Perception & Psychophysics *37*, 1–7.

Frazier, L., Carlson, K., Clifton, C.J. (2006). Prosodic phrasing is central to language comprehension. Trends in Cognitive Science *10*, 244–249.

Fujii, S., Schlaug, G. (2013). The Harvard Beat Assessment Test (H-BAT): a battery for assessing beat perception and production and their dissociation. Frontiers in Human Neuroscience *7*, 771.

Geiser, E., Sandmann, P., Jäncke, L., Meyer, M. (2010). Refinement of metre perception - training increases hierarchical metre processing: training effects on metre perception. European Journal of Neuroscience *32*, 1979–1985.

Grahn, J.A. (2012). Neural mechanisms of rhythm perception: current findings and future perspectives. Topics in Cognitive Science *4*, 585–606.

Grahn, J.A., Brett, M. (2007). Rhythm and beat perception in motor areas of the brain. Journal of Cognitive Neuroscience *19*, 893–906.

Grahn, J.A., McAuley, J.D. (2009). Neural bases of individual differences in beat perception. NeuroImage *47*, 1894–1903.

Grahn, J.A., Rowe, J.B. (2009). Feeling the beat: premotor and striatal interactions in musicians and nonmusicians during beat perception. Journal of Neuroscience *29*, 7540–7548.

Hannon, E.E., Snyder, J.S., Eerola, T., Krumhansl, C.L. (2004). The role of melodic and temporal cues in perceiving musical meter. Journal of Experimental Psychology: Human Perception and Performance *30*, 956–974.

Hasegawa, A., Okanoya, K., Hasegawa, T., Seki, Y. (2011). Rhythmic synchronization tapping to an audio–visual metronome in budgerigars. Scientific Reports *1*, 120.

Hattori, Y., Tomonaga, M., Matsuzawa, T. (2013). Spontaneous synchronized tapping to an auditory rhythm in a chimpanzee. Scientific Reports *3*, 1566.

Henry, M.J., Herrmann, B., Grahn, J.A. (2017). What can we learn about beat perception by comparing brain signals and stimulus envelopes? PLoS One *12*, e0172454.

Hoeschele, M., Merchant, H., Kikuchi, Y., Hattori, Y., ten Cate, C. (2015). Searching for the origins of musicality across species. Philosophical Transactions of the Royal Society B: Biological Sciences *370*, 20140094.

Iversen, J., Patel, A. (2008). The Beat Alignment Test (BAT): Surveying beat processing abilities in the general population. Proceedings of the 10th International Conference on Music Perception and Cognition. Sapporo, Japan. 465-468.

Jones, M.R. (1976). Time, our lost dimension: toward a new theory of perception, attention, and memory. Psychological Review *83*, 33.

Jones, M.R., Boltz, M. (1989). Dynamic attending and responses to time. Psychological Review *96*, 459–491.

Large, E.W. (2000). On synchronizing movements to music. Human Movement Science *19*, 527–566.

Large, E.W., Gray, P.M. (2015). Spontaneous tempo and rhythmic entrainment in a bonobo (*Pan paniscus*). Journal of Comparative Psychology *129*, 317–328.

Large, E.W., Palmer, C. (2002). Perceiving temporal regularity in music. Cognitive Science *26*, 1–37.

Longuet-Higgins, H.C., Lee, C.S. (1984). The rhythmic interpretation of monophonic music. Music Perception *1*, 424–441.

Mach, E. (1887). Beiträge zur analyse der empfindungen. Revue Philosophique de La France Et de l'Etranger *23*, 80–83.

McAuley, J.D. (1999). The effect of tempo and musical experience on perceived beat. Australian Journal of Psychology *51*, 176–187.

McAuley, J.D. (2010). Tempo and rhythm. In M.R. Jones, R.R. Fay, A.N. Popper, (Eds.) Music Perception. New York, NY: Springer New York, pp. 165–199.

McAuley, J.D., Henry, M.J., Tkach, J. (2012). Tempo mediates the involvement of motor areas in beat perception. Annals of the New York Academy of Sciences *1252*, 77–84.

Müllensiefen, D., Gingras, B., Stewart, L., Musil, J.J. (2012). Goldsmiths Musical Sophistication Index (GOLD-MSI) v1.0.

Nettl, B. (2000). An ethnomusicologist contemplates universals in musical sound and musical culture. In N.L. Wallin, B. Merker, S. Brown (Eds.) The origins of music. London: Massachusetts Institute of Technology Press, pp. 463-472.

Parncutt, R. (1994). A perceptual model of pulse salience and metrical accent in musical rhythms. Music Perception *11*, 409–464.

Patel, A.D., Iversen, J.R. (2014). The evolutionary neuroscience of musical beat perception: the Action Simulation for Auditory Prediction (ASAP) hypothesis. Frontiers in Systems Neuroscience *8*, 57.

Patel, A.D., Iversen, J.R., Bregman, M.R., Schulz, I. (2009). Experimental evidence for synchronization to a musical beat in a nonhuman animal. Current Biology *19*, 827–830.

Povel, D.J., Okkerman, H. (1981). Accents in equitone sequences. Perception & Psychophysics *30*, 565–572.

Rohenkohl, G., Coull, J.T., Nobre, A.C. (2011). Behavioural dissociation between exogenous and endogenous temporal orienting of attention. PLoS One *6*, e14620.

Sakai, K., Hikosaka, O., Miyauchi, S., Takino, R., Tamada, T., Iwata, N. K., Nielsen, M. (1999). Neural representation of a rhythm depends on its interval ratio. Journal of Neuroscience *19*, 10074-10081.

Schachner, A., Brady, T.F., Pepperberg, I.M., and Hauser, M.D. (2009). Spontaneous motor entrainment to music in multiple vocal mimicking species. Current Biology *19*, 831–836.

Su, Y.-H., Pöppel, E. (2012). Body movement enhances the extraction of temporal structures in auditory sequences. Psychological Research *76*, 373–382.

Temperley, D., Bartlette, C. (2002). Parallelism as a factor in metrical analysis. Music Perception *20*, 117–149.

Vuust, P., Witek, M.A.G. (2014). Rhythmic complexity and predictive coding: a novel approach to modeling rhythm and meter perception in music. Frontiers in Psychology *5*, 1111.

Vuust, P., Pallesen, K.J., Bailey, C., van Zuijen, T.L., Gjedde, A., Roepstorff, A., Østergaard, L. (2005). To musicians, the message is in the meter. NeuroImage *24*, 560–564.

Warren, R.M. (1993). Perception of acoustic sequences: global integration versus temporal resolution. In McAdams, S., Bigand, E. (Eds.), Thinking in sound: the cognitive psychology of human audition. New York, NY: Clarendon Press/Oxford University Press, pp. 37–68.

van der Weij, B., Pearce, M.T., Honing, H. (2017). A probabilistic model of meter perception: simulating enculturation. Frontiers in Psychology *8*, 824.

Wilson, M., Cook, P.F. (2016). Rhythmic entrainment: why humans want to, fireflies can't help it, pet birds try, and sea lions have to be bribed. Psychonomic Bulletin & Review *23*, 1647–1659.

Winkler, I., Haden, G.P., Ladinig, O., Sziller, I., Honing, H. (2009). Newborn infants detect the beat in music. Proceedings of the National Academy of Sciences *106*, 2468–2471.

Zarco, W., Merchant, H., Prado, L., Mendez, J.C. (2009). Subsecond timing in primates: comparison of interval production between human subjects and rhesus monkeys. Journal of Neurophysiology *102*, 3191–3202.

Chapter 3

3 Introduction

3.1 Comparative Studies of Beat

Our understanding of how the human brain perceives and produces music is far from complete. Cognition of music depends a host of distinct capacities for sensing and processing the acoustic and structural properties of music, many of which extend beyond the auditory domain. For example, music has remarkable, mysterious power to make humans move to it. The temporally regular pulse – "the beat" – that humans can sense and move to in music depends on contributions from the motor system and involves the brain's facilities for prediction and timing (Grahn, 2012). It seems unlikely that the many musical capacities of humans all evolved simultaneously and are exclusive to a single species (Patel & Demorest, 2013). By examining cognition of other non-human animals, it may be possible to make inferences about the individual evolutionary histories of certain capacities, and this research may in turn provide a way to study the evolution of human musicality (Fitch, 2006; McDermott & Hauser, 2005).

If the capacity to perceive beat is universal in humans, what about in non-human animals? Over the last century a growing body of literature has surveyed the animal kingdom in search of evidence to show the capacity for beat perception exists in other species. If positive evidence is found, this may potentially enable further studies in an animal model in which more invasive methodology may be applied to shed light on the development and neuroanatomical substrates of beat perception. Further, the exploration of beat perception in a range of species will facilitate comparative analyses in order to determine its adaptive functions.

Experimental research on beat perception in non-human animals has used limited methodology to test only a select few species. Akin to behavioural tasks that test beat ability in humans, previous cross-species studies can be divided into those that aim to directly examine perception of a beat, and others that examine production of movement synchronized to a beat. For perception-based tasks, the animal must attend towards an auditory or visual stimulus and make judgements about regularities found in its structure. Inferences can be made about perceptual processes in non-human animal subjects based on their behavioural responses. Perceptual tasks have included discriminations between regular and irregular patterns (e.g., van der Aa et al., 2015; ten Cate et al., 2016) and odd-ball detection tasks (e.g., Honing et al., 2012) although no behavioural paradigms have been used consistently across species. For production tasks, a non-human animal must entrain the timing of its body movement to regularity present in an external rhythmic stimulus. Synchronized behaviour may theoretically take any form, but some may be species-specific. Examples include pecking in budgerigars (Hasegawa et al., 2011), foot-lifting in a cockatoo (Patel et al., 2009), head bobbing in a sea lion (Cook et al., 2013) and trotting in horses (Bregman et al., 2013).

In previous studies that have examined the sensitivity of non-human animals to auditory regularities, the acoustic stimuli usually contain periodicities spanning multiple properties of sound, such as regular variations of the frequency, spectra or amplitude of recurring notes. However, relatively little research has looked at whether other animals experience internal, psychological pulses (a beat pattern). Meter and beat have been modelled extensively in humans (see McAuley, 2010 for a review of this literature) but virtually nothing is known about their perception in other species. In this thesis I follow the Povel & Essens clock-induction model to produce auditory rhythms that contain a regular beat (Povel & Essens, 1985). The model states

that the presence of temporally regular accents (instances when a note is emphasized or salient relative to its neighbours) contributes to the induction of a beat in humans. It is unknown whether other species perceive temporal accents in rhythms or if accent structure may contribute to beat induction in non-humans.

3.2 Songbirds: The Untapped Beat Perceivers?

A leading theory on the existence of beat perception ability in animals considers a hypothetical connection with vocal learning, a rare trait so far found in only five groups of mammals (humans, cetaceans, elephants, bats and seals) and three groups of birds (parrots, passerines and hummingbirds). The brains of vocal learning species feature specialized auditory-motor cortical networks that are used to integrate incoming auditory temporal information with flexible motor control of the vocal production organ (Jarvis, 2007). According to the vocal learning hypothesis, this auditory-motor connectivity is necessary for the precise coupling of auditory and motor timing in beat perception and synchronization (Patel, 2006). The hypothesis accounts for both positive evidence of beat synchronization in multiple vocal-learning parrot species (Hasegawa et al., 2011; Patel et al., 2009; Schachner et al., 2009) and the apparent absence of beat synchronization ability in non-human primates, which do not flexibly learn their vocalizations (Zarco et al., 2009). However, sensitivity to beat has not been experimentally demonstrated in any other vocal learning groups beyond humans and parrots.

A sister group to parrots is the passerines, a diverse order of songbirds that fit the conventional definition of imitative vocal learning. Second to human speech, birdsong is the most widely studied of vocal communication systems. Research on songbirds' neuroanatomy, on their perception of sound and on their development and learning has taught us a great deal about vocal learning in this group. A collection of structures and pathways have been identified as

homologues in the brains of songbirds, parrots and hummingbirds that are functionally adapted for vocal learning and are thought to bear similarities between these groups (Chakraborty & Jarvis, 2015). Significant variation exists within passerines in the complexity, flexibility and timing of vocal learning (Slater, 1983). For instance, European starlings (*Sturnus vulgaris*) retain their ability to learn new vocalizations across their lifespan (Mountjoy & Lemon, 1995) and both sexes produce elaborate, hierarchical song (Pavlova et al., 2005). This makes starlings unlike many other passerine species, including the domesticated and well-studied zebra finch (*Taeniopygia guttata*) in which only male birds sing a relatively simple song and vocal flexibility is restricted to a sensitive period for learning during early life (Braaten et al., 2006). In consideration of the vocal learning hypothesis, I selected mature starlings as a test species since their capacity for vocal learning is maintained as adults.

A wealth of information is known about auditory processing in starlings. Numerous studies have examined starlings' perception of frequencies, spectra, intensities, harmonies and many aspects of auditory timing (see Hulse et al., 1992 for a review). Hulse and Cynx (1985) found that starlings preferentially used absolute cues for discriminating pitch, but that perceptual invariance for pitch patterns was possible across a limited range of learned transformations (Hulse & Cynx, 1985). Starlings' perception of temporal patterns has been partly characterized, including their use of grouping principles in the perception of discrete pattern events, their ability to discriminate regular from irregular stimuli, and their ability to segregate auditory streams using temporal information (Braaten & Hulse, 1993; Hulse et al., 1984; Itatani & Klump, 2011). Starlings can discriminate harmonic complexes with greater temporal resolution than humans (Dooling et al., 2002). Work by others has examined starlings' sensitivity to interval timing and found the species to be highly adept at learning absolute interval durations (Maier & Klump,

1990). The capacity of this species to learn abstract concepts based in relative (or associative) timing has been explored in a few experiments that have mostly used artificial arrangements of conspecific vocalizations (Comins & Gentner, 2014; Gentner et al., 2006). Collectively, findings of this research support that starlings, like most animals, prefer to attend to individual pattern elements rather than global pattern structures in the auditory domain; but the capacity to learn some pattern rules is thought to exist in this species and may be recruited under specific circumstances (Abe & Watanabe, 2011; Gentner & Hulse, 2000).

Whether starlings are sensitive to beat or meter is unclear. No songbirds are known to spontaneously entrain body movement to an auditory beat as observed in parrots. To examine the capacity for beat perception in songbirds, I apply a novel method that tests whether an animal can detect regular accent structure in auditory patterns. The aim of the first experiment of this chapter was to determine whether starlings could learn a discrimination between metric simple (MS) and metric complex (MC) stimuli that was performed in the previous chapter by human participants. A categorization procedure was implemented using operant conditioning. If the vocal learning hypothesis is supported, I predicted that starlings (as a vocal learning species) would possess the capacity for beat perception needed to learn this discrimination. A second follow-up experiment aimed to examine the subjects' use of a strategy for discriminating temporal patterns, with specific focus on their attention to absolute or relative cues.

3.3 Methods

3.3.1 Auditory Stimuli

The acoustic equitone stimuli used in this experiment, as well as in the experiment described in Chapter 2, were designed to be suitable for both human participants and songbird subjects. Physical properties of these sounds were chosen to be compatible with sensitive

auditory ranges for both species. For the frequency of the pure tones, an average frequency was selected within the normal vocal range for starlings while still comfortable for listening by humans. This value was determined by applying a Fourier analysis to examine the frequencies present in a sample of 17 recordings of individual starlings' song obtained from the Cornell Lab of Ornithology's online database. Recordings were analyzed in Matlab 2017b in order to identify frequencies with the greatest average power in the signal. Secondly, I analyzed the recordings of starling song to look for regularly-timed onsets of vocalizations present in the amplitude envelope of the signal. This information was used to approximate an appropriate rate for the rhythmic stimuli based on the tempo of regular elements in starling song. In reviewing the bioacoustics literature, I found little to no research that has investigated regularities present in the timing of note onsets in birdsong.

The frequency bin with the greatest power was determined to be 1510 Hz; the frequency of the tonal stimuli was rounded to 1500 Hz. A Hilbert transformation was applied to each recording to produce an amplitude envelope, which was then analyzed using Matlab's peakfinder function. The analysis confirmed what had already seemed obvious upon visual inspection of the recordings: some of the local maxima in the envelop were separated by approximately equal inter-onset intervals during bouts of repeating song elements, ranging from 3-8 discrete elements in length. Among the instances of regularly timed onsets that were found in the recordings, the average length of the intervals between peaks was 171 ms. For the purpose of the comparative experiments on beat perception, I considered this interval duration (171 ms) to be approximately similar to the smallest interval (220 ms) used in the experimental stimuli, which was chosen because it falls within the upper range of rates at which humans will perceive a beat, the total range of which is from about 1.5 to 5.0 beats per second (Handel, 1989). This interval duration

found in starlings' recorded song was thus used to select a suitable rate for presenting rhythmic tonal stimuli to this species. However, future research is needed to determine whether starlings and other songbirds prefer certain rates in auditory rhythms, particularly towards artificial sounds like those used here.

3.3.2 Subjects

Eight experimentally naïve, wild-caught European starlings of unknown age were used in this study. The birds were obtained in Port Rowan, Ontario, where they were captured near a feeder site. A total of 8 large, healthy birds (4 males: 4 females) were selected for inclusion in this study. Based on their size and the appearance of their plumage, all of the subjects were adults at the time of capture (Feare, 1984). Sexing was determined visually based on sexual dimorphism in starlings' beak coloration in spring. In tribute to the musical theme of this work, the subjects were assigned labels after the namesakes of classical composers. These labels are used here for the purpose of reporting individual subject data.

Care and treatment of the birds strictly followed guidelines from Canadian Council on Animal Care (CCAC) and a protocol approved by the animal care committee at the University of Western Ontario. The birds were housed within individual cages in a temperature-controlled room. The cages used to house the birds were furnished with environmental enrichment, including plastic toys, water baths and perches fabricated from tree branches. The light:dark cycle in the room was matched to local outdoor sunrise and sunset times to as to maintain the birds on their natural photoperiod throughout the duration of their captivity.

The birds underwent an initial quarantine period that spanned several weeks, throughout which they were treated for parasites and monitored for general health. Birds were fed a diet consisting of Purina Golden starter for poultry, which was initially provided *ad libitum* in the

home cage, and mealworms, which were supplemented as positive reinforcement for desired behavior. This high availability of food resulted in all of the birds gaining body mass until reaching an equilibrium. In order to motivate subjects to participate in the experiments in exchange for food rewards, the birds' daily allocated food was restricted. Each tested bird was maintained at 85 percent of its maximum body weight recorded during *ad libitum* feeding. The birds were weighed and inspected for health on a weekly basis, and their quantity of total daily food was adjusted proportionally to maintain them at their target weight.

I trained the starlings to enter and exit a transfer carrier in exchange for mealworms, reducing the need for potentially stressful physical handling while moving them to and from the testing apparatus. One starling persistently refused to enter the carrier and required physical handling before and after each session (to which it eventually habituated).

3.3.3 Operant Apparatus

The experiments were conducted using four operant testing boxes (30 x 24 x 29 cm) produced by MED Associates Inc., St Albans, Vermont, USA (Figure 3.1). The boxes were positioned atop shelves within standalone sound-attenuating chambers. Each box was run on an individual power supply and computer. The computers were connected via a switch to a single display monitor mounted on the exterior of a chamber door, allowing for active monitoring during testing sessions. The acoustic stimuli were presented through Logitech desktop speakers (Freemont, CA, USA) positioned adjacent to the boxes; the volume was fixed at 70 dB and checked periodically using an A-weighted sound pressure level meter configured to a slow time weighting and positioned at the level of the bird's head.

Each testing box featured three translucent response keys (diameter 2.5 cm) located on the interior walls that the birds were trained to peck in exchange for food rewards. The first key

was mounted in the center of the rear side of the box and was pecked by the bird to initiate trials. The second and third response keys were mounted on the opposite wall, on either side of the food hopper, and were labelled left and right respectively. Between the response keys was a port (opening 5 x 6 cm) used to deliver food rewards from an external hopper, which would shift upwards during the feeding interval enabling the bird to access its contents. The box was illuminated using a house light that would turn off briefly following incorrect responses . The response keys, house light and food hopper were attached to a microcontroller (8 Input, 16 output SmartCtrl, Med Associates Inc.) and a computer running MED-PC IV software (Med Associates Inc.) for controlling data input and output. Water was available at all times through a bottle attached to the wall opposite to the food hopper. For all training and testing procedures described in this Chapter, the subjects were placed inside of the operant testing boxes each day for 2-hour sessions, always starting at the same time daily.

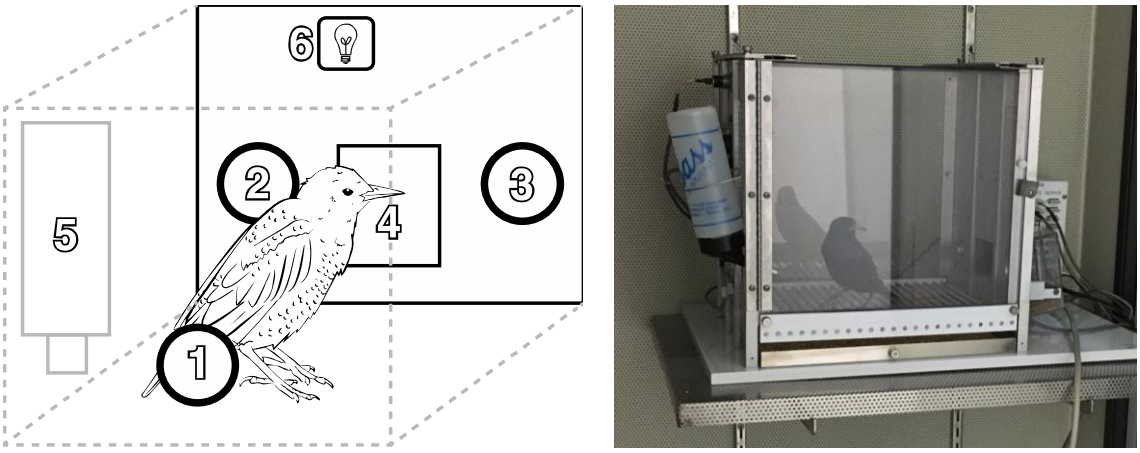

Figure 3.1. A schematic of the operant testing boxes used in the experiments, labelled as follows: 1 the trial initiation key; 2 the left response key; 3 the right response key; 4 the delivery port to access the food hopper; 5 the water bottle available throughout the session; 6 the house light, which turned off following error responses. The photograph on the right shows a pilot subject, Beethoven, inside of the apparatus housed within a sound attenuating chamber.

3.3.4 Shaping and Training Procedure

All subjects underwent an initial training procedure in which they were incrementally taught to use of the apparatus over several weeks. Subjects began habituation to the operant box by learning to access the food hopper within the allotted feeding interval (first 30 seconds, then 15 seconds, then 7 seconds, finally 3 seconds) which would alternate between the open/closed position automatically every 30 seconds. Next the subjects were trained to peck the keys in the chamber. Initially the birds' attention was drawn towards a key by taping a mealworm onto the rear of the transparent plastic backing. Each peck registered by the key would activate the food hopper. Once the birds were reliably pecking the baited key, this cue would be removed for subsequent sessions.

The birds first learned to peck the trial start key for reinforcement. Secondly, the birds learned that pecking of the trial start key would result in a sound stimulus playing (a single metric simple pattern), and that reinforcement would only occur upon subsequent pecking of the left response key within 8 seconds of sound offset – the key was again cued using a mealworm. Thirdly, the birds learned that pecking of the trial start key would play an alternate sound stimulus (a single metric complex pattern), but now only the right response key was reinforced. Some of birds underwent several training sessions that alternated between all-MS and all-MC presentations to ensure the subjects learned to attend to the sound stimulus before responding. In the final stage of peck training, once all of the keys were being used by the bird, pecking of the trial start key would result in random presentations of either the MS or MC stimulus, to be followed by pecking the appropriate response key for delivery of food reinforcement.

When the subject was consistently pecking all three keys, a "punishment" following response errors was gradually introduced, increasing in duration across three sessions. If the

subject pecked the incorrect response key following a stimulus presentation, the light in the chamber would turn off for a timeout period (25 seconds) which served as a feeding opportunity cost. Each timeout was followed by a correction trial in which the same stimulus that was presented on the previous error trial was repeated. Any trial in which neither response key registered pecks in the eight seconds following sound offset was labelled as an omission; no feedback was produced, and a correction trial would begin following the next peck registered by the trial start key.

At the end of the experimental sessions, the birds were placed back in their home cage without food for approximately 2 hours before being fed the remainder of their allocated daily food amount. This schedule was incorporated after pilot testing suggested the birds had learned to expect that food would be provided in their dish afterwards, and I observed a marked drop in trial initiation and responding towards the end of each session.

3.3.5 Experiment 1

In this experiment I aimed to train and test starlings on a discrimination between metric simple (MS) and metric complex (MC) patterns using a categorization task that was equivalent to the experiment with human subjects described in Chapter 2. Like in the human experiment, the initial experimental strategy consisted of training the birds to discriminate between a subset of MS and MC patterns, then testing their ability to generalize the learned rule to novel patterns. I predicted that if songbirds are capable of perceiving regular temporal accents – "the beat" – in keeping with the vocal learning hypothesis, then the subjects would learn to discriminate the stimuli on a similar basis to humans. Theoretically, according to the Povel & Essens clock-induction model, this is achieved by the subject internally fitting a metrical 4-clock to a rhythm and comparing the position of perceived accents with the units of the clock (Povel & Essens,

1985). More realistically, the birds would need to learn that patterns in which accents are perceived at regular points in time belong to a distinct category (the metric simple) from patterns that do not fit this criterion (the metric complex). This discrimination between simple and complex tests the ability of the subject to discriminate between metric categories. If a non-human animal can learn this task, it would provide positive evidence of a capacity for beat perception in the tested species.

On the other hand, it is possible that the subjects could fail to improve in accuracy across many trials. This outcome may be interpreted in a few ways. Perhaps the birds fail to differentiate the simple and complex rhythms due to a lack of conceptual learning, leading them to attend to the wrong features or develop an irrelevant strategy. If the birds learn the initial discrimination but fail to generalize, maybe it is because they are overly poor beat perceivers and are unable to consistently find a regular beat in the metric simple rhythms, which may result in bias towards the "no beat" response. Or maybe the birds are actually adept beat finders, able to find a beat in all of the rhythms including metric complex, which would result in a bias towards the "beat" response. In any case the birds must grasp conceptual associations between the metric categories and the two available response keys. Failure to learn these associations would render it impossible to interpret any evidence for learning of metric categories or for beat perception.

Crucially, this comparative experiment assumed that songbirds have the capacity to perceive temporal accents in auditory rhythms. No research has ever determined whether songbirds perceive temporal accents, and little is known in general about the sensitivity of other animals to metrical structure. There are few conceivable ways to test an animal's capacity to perceive accents in sounds. The comparative approach used here provides a starting point in

testing whether perceptual rules that govern rhythm processing and beat induction in humans are common in other species.

For this experiment, the same pool of 44 equitone stimuli described in Chapter 2 was to be used. If the birds had successfully learned the rule underlying the discrimination in their training (which would imply that they are sensitive to regular temporal accents) then I predicted that as subjects generalize the rule to novel stimuli, I would observe faster learning and a greater proportion of correct responses than would be expected if theywere simply memorizing the trial feedback provided for each response.

3.3.5.1 Pilot Training

Upon completing the habituation and shaping procedures, three pilot subjects (Chopin, Debussy, Beethoven) began training on a discrimination between a single metric simple (42231) and single metric complex (23142) stimulus, paired with the left and right response keys respectively. Each stimulus was presented for 7 seconds, containing two iterations of the pattern separated by a brief silent pause of 1.8 seconds. Between these pilot sessions various parameters of the experiment were optimized to further motivate the subjects to behave and to ensure compatibility of the operant apparatus with the tested species. The birds appeared to learn to correctly use the apparatus. However, with the finalized parameters in place, the birds still did not exceed chance-level responding on a discrimination between the single MS and MC patterns after several weeks of daily training sessions.

3.3.5.2 Isochronous-Triplet Discrimination

To confirm the effectiveness of the operant training procedure, the three pilot subjects and five additional birds (Liszt, Schubert, Vivaldi, Tchaikovsky, Bach) began training on a second auditory pattern discrimination that was designed to be easier to learn. The birds were

presented with two novel patterns constructed with the same pure tones as in the MS-MC set and of the same overall stimulus duration (7 seconds). These two stimuli were differentially paired with the left and right response keys, similar to training of the pilot birds. The first stimulus was an isochronous pattern with inter-onset intervals of 660 milliseconds. The second stimulus was a "triplet" pattern in which three tones would play in quick succession (between them inter-onset intervals of 220 milliseconds) separated by a longer silent interval (660 milliseconds). The patterns can be represented with the notation 66666 for isochronous and 226226 for triplet. When humans listen to the triplet pattern the tones become perceptually grouped into threes with a galloping rhythm (hence the label). There is some experimental evidence to suggest that starlings may also perceptually group discrete auditory events (e.g., Braaten & Hulse, 1993) but the precise rules that starlings use are not clearly defined. Regardless, perceptual grouping was not required for the isochronous-triplet discrimination to be learned. Previous work has demonstrated that a discrimination between these pattern configurations can be learned by starlings (MacDougall-Shackleton et al., 1998).

3.3.5.3 Metric Simple-Complex Discrimination

Immediately following the isochronous-triplet discrimination the birds were transferred to the same discrimination from the pilot training: a single MS (42231) and MC (23142) pattern. I intended to incrementally work the birds up to a discrimination of twelve training stimuli, which were randomly selected for each bird from the same pool of 44 equitone patterns used in the comparative experiment with human participants described in Chapter 2. That these specific stimuli were used as the initial starting point for the birds' training on the MS-MC discrimination was a mostly arbitrary choice. I opted to start the birds with these two patterns because they were relatively short (containing only 5 intervals as opposed to 6 or 7) and because they were

generated from the same parent set of intervals, meaning that they could not be discriminated simply on the basis of a single interval being exclusive to one of the patterns.

One subject advanced upon meeting the accuracy criterion on the first MS/MC discrimination to next be presented with two additional novel stimuli: a second MS and second MC pattern, both combinations generated from the same set of intervals as the previous two (Table 3.1). Presentations of the "new" stimuli were randomly intermixed with the "old" stimuli, and erroneous responses were again followed by trial feedback and correction trials. These four stimuli were presented across 17 sessions.

Table 3.1. Additional MS and MC patterns presented to one European starling subject, Liszt, as a test of discrimination generalization from the "old" stimuli to the "new" stimuli. All four patterns were derived from the parent interval set 12234.

"Old" Stimuli		"New" Stimuli	
Metric Simple	Metric Complex	Metric Simple	Metric Complex
42231	23142	22413	14232

3.3.6 Experiment 2

To confirm the effectiveness of the operant training procedure used in Experiment 1, the starlings were transferred to a relatively simple discrimination between two patterns of tones: an isochronous pattern (represented by the notation 66666) in which a single inter-onset interval was used, and a triplet pattern (represented by the notation 226226) in which shorter and longer intervals were combined. In order to probe the starlings' sensitivity towards particular features of temporal auditory patterns, I used the isochronous and triplet stimuli again for the baseline discrimination of a second experiment. Due to a technical requirement of the program used to create the sound files, the base interval for the metrical stimuli used in the previous experiments

was adjusted slightly, from 1 = 220 milliseconds to 1 = 240 milliseconds. Also, the notation for intervals was switched so that 1 = 120 milliseconds and 2 = 240 milliseconds.

This second experiment considered the subjects' responses to a set of probe stimuli in which the temporal properties of the two learned baseline patterns were modified into various configurations. If the starlings were utilizing a strategy while learning or listening to the stimuli, I reasoned that it might be influenced by a bias to attend towards certain temporal features. Given the large individual differences observed in their performance of the discriminations, it seemed possible that the subjects had developed alternate strategies. This second experiment was intended to assess the sensitivity of starlings to features of temporal patterns, and to offer some diagnostic insight into how the stimuli from Experiment 1 were perceived.

3.3.6.1 Subjects

The same eight starlings that were used in the previous experiment were included as subjects. However, one bird, Chopin, had prolonged difficulty reaching criterion on the discrimination training and maintaining the learned associations throughout testing. Across several sessions Chopin showed extinction for both response keys and would often peck the same key on every trial regardless of the stimulus. Chopin proceeded to complete only part of this experiment; data from this bird is depicted in figures for between-subject comparisons but should be interpreted conservatively.

3.3.6.2 Baseline Training

The subjects returned to the same isochronous-triplet discrimination from the previous experiment. The birds again learned to associate the isochronous pattern with the left response key and the triplet pattern with the right response key. Each of the birds underwent baseline training until a criterion of 75 percent of trials correct was met across three sessions. At this point

a variable reinforcement schedule was gradually introduced such that feedback would only follow responses on 80 percent of trials. Each time the subject pecked the trial initiation key, there was a 20 percent probability of a probe trial occurring in which a novel probe stimulus was presented. On probe trials, pecks to the response keys were recorded but would lead directly into the next trial without the delivery of any reinforcement. The lack of feedback made it impossible for the birds to simply memorize which response was correct for the most recently presented stimulus. Approximately 50-60 probe trials occurred in each testing session, depending primarily on the subject's rate of responding.

A set of novel stimuli were presented on the probe trials. In each test session only a single probe stimulus was presented, embedded among more frequent presentations of the baseline patterns. The probe presentation order was pseudorandomized between subjects. Accuracy on the baseline discrimination, which made up 80 percent of trials in the test sessions, was recorded separately from responses to the novel probe stimuli. Following each test session, subjects were returned to the baseline discrimination for two sessions (with the variable reinforcement schedule kept in place) before proceeding to the next probe stimulus.

3.3.6.3 Probe Stimuli

To explore the subjects' use of a perceptual strategy for discriminating temporal patterns, a set of 12 probe stimuli was generated by modifying the durations of inter-onset intervals that comprised the isochronous (666666) and triplet (226226) baseline patterns (Table 3.2). Six probe stimuli were produced by transforming the tempo of the baseline patterns: faster and slower versions of the isochronous and triplet patterns were created by reducing or increasing the durations of inter-onset intervals, while maintaining the ratio between intervals within each pattern. If the starlings were using a strategy based on the rate of the stimuli, then the faster

probes would be associated with the faster triplet baseline pattern, and slower probes would be associated with the slower isochronous baseline pattern. Four probe stimuli were generated by modifying the ratios of intervals in the triplet pattern: the interval within a triplet of tones was made longer or shorter relative to the interval between triplets. If the starlings were perceiving the patterns in a relative sense, then modifications of the ratios within the patterns could disrupt generalization from the baseline stimuli, and this might be reflected in a more variable distribution of responses within or between subjects. Lastly, two probe stimuli were derived from the baseline triplet pattern by altering the number of tones contained within a perceptual grouping, such that quadruplets or dyads of tones, rather than triplets, were separated by a relatively long between-grouping interval. If the starlings were perceptually grouping the patterns and could extend the concept of grouping to include larger or smaller groups (contrary to other group sizes being identified as isochronous) then I expected that these modified stimuli would be consistently related to the baseline triplet pattern.

Table 3.2. The twelve probe stimuli used in the second operant experiment described using integer notation. For all stimuli, an interval length of 1 = 120 milliseconds. Dashes represent identical pure tones. The stimulus set includes patterns that were created in one of two ways: 1. By multiplying the length of all intervals in the baseline patterns by the same factor, yielding fast and slow tempi versions of the patterns; 2. By modifying the ratio between the intervals within the baseline patterns.

		Probe Transformation Type		
		Tempo (fast)	Tempo (slow)	Other Ratios
Pattern Category	Isochronous (baseline 6-6-6-6-6-6)	2-2-2-2-2-2 3-3-3-3-3-3 4-4-4-4-4-4	9-9-9-9-9-9	2-2-3-2-2-3 2-2-9-2-2-9 5-5-8-5-5-8
	Triplet (baseline 2-2-6-2-2-6)	1-1-3-1-1-3	4-4-12-4-4-12	2-6-6-2-6-6 2-2-2-6-2-2-2-6 2-6-2-6-2-6

3.4 Results

3.4.1 Experiment 1

3.4.1.1 Isochronous-Triplet

All eight subjects learned the discrimination between the isochronous and triplet patterns and met the accuracy criterion of 75 percent of trials correct across three sessions (average = 25.88 sessions, SD = 10.64 sessions). The subject to reach criterion the fastest was Liszt after 16 sessions, and the slowest subject was Chopin after 41 sessions. Overall, the three pilot subjects (Chopin, Debussy, Beethoven) who had previously trained on MS and MC patterns took longer to transfer to the isochronous-triplet discrimination. Discriminative accuracy was determined to be significantly above chance level using a binomial test (Figure 3.2). The learning of the

isochronous-triplet discrimination by all eight subjects was taken as evidence that the operant procedure described here was at least effective for training the birds to discriminate between two acoustic patterns outside of the experimental MS/MC set.

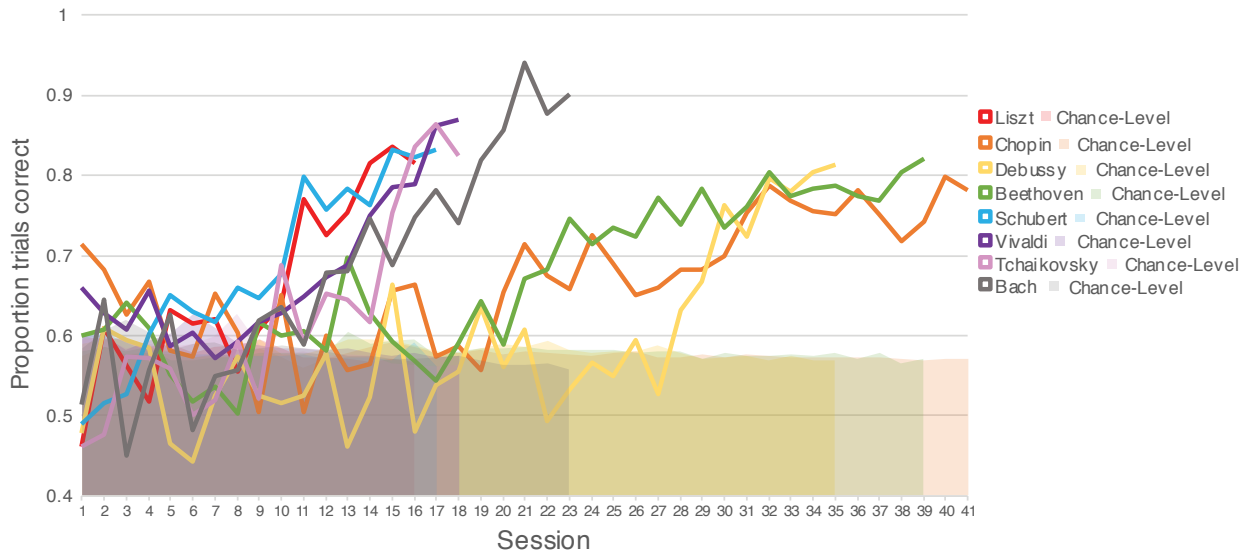

Figure 3.2. Learning of the isochronous-triplet discrimination by European starlings in an operant categorization procedure. The vertical axis shows the proportion of trials correct excluding correction trials; the horizontal axis shows session number. Lines represent the proportion responses correct for individual subjects across multiple sessions, excluding responses made on correction trials. Shaded areas represent the proportion of correct responses needed to exceed chance-level, for each bird, within each session, determined using a binomial test. The graph depicts all lines increasing above their accompanying shaded area, indicating that the birds' discrimination accuracy was significantly above chance.

3.4.1.2 Metric Simple-Complex

Seven of the eight birds failed to transfer to a discrimination between a single MS and MC stimulus (Figure 3.3). The birds each underwent a minimum of 35 daily testing sessions (mean 43 sessions, SD = 5.19) on consecutive days. Some subjects received additional sessions having begun the transfer earlier upon reaching criterion on the isochronous and triplet pattern discrimination.

That the birds mostly failed to learn the MS and MC discrimination matches the earlier failure of the three pilot subjects to acquire the same discrimination. Notably, one subject, Liszt, did eventually learn to discriminate two patterns, meeting the accuracy criterion after 46 sessions. A second bird, Vivaldi, appeared to make some progress after 50 sessions. However, the improvement of these two birds was markedly slower than the acquisition of the previous isochronous and triplet discrimination, which was learned relatively faster by all of the subjects. Given the difficulty the birds exhibited with a discrimination of only two patterns, I expected that additional stimuli would require many more sessions of training, if they were to be learned at all.

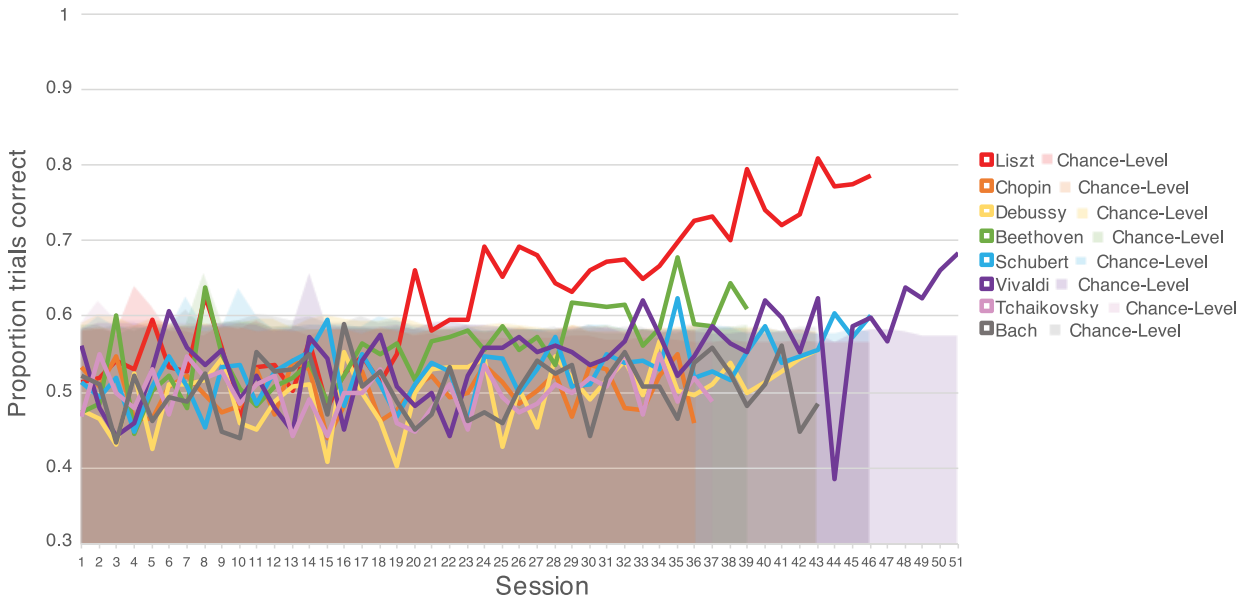

Figure 3.3. Failed acquisition of a discrimination between two stimulus patterns, metric simple (42231) and metric complex (23142), by European starlings using a categorization operant procedure. The vertical axis shows the proportion of trials correct excluding correction trials; the horizontal axis shows session number. Lines represent the proportion responses correct for individual subjects across multiple sessions, excluding responses made on correction trials. Shaded areas represent the proportion of correct responses needed to exceed chance-level, for each bird, within each session, determined using a binomial test. Each bird was tested for a minimum of 35 sessions. The only subject to meet the accuracy criterion to advance and to consistently respond correctly above chance-level was Liszt, shown in red.

3.4.1.3 Generalization to Novel Patterns

A single bird, Liszt, advanced to a discrimination between four training patterns. Upon the addition of two "new" stimuli, discriminative accuracy for the "old" stimuli dropped to chance level responding by the seventeenth session (Figure 3.4).

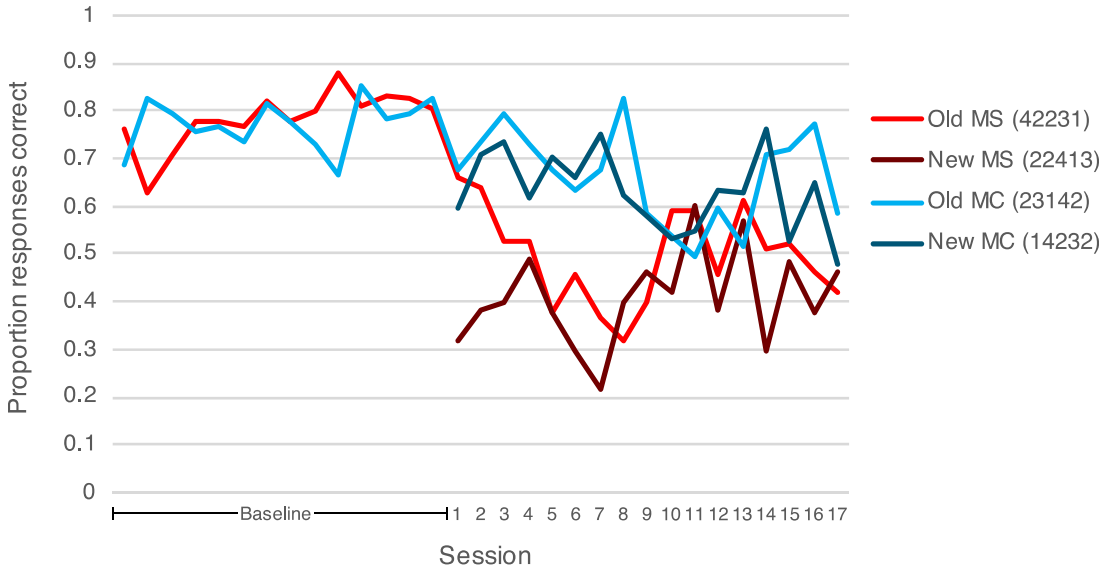

Figure 3.4. Response data obtained from Liszt, a single starling subject that advanced from the first training MS-MC discrimination of Experiment 1 to a discrimination between four stimuli. The vertical axis shows the proportion of trials; the horizontal axis shows session number. Lines represent the proportion responses correct for individual stimuli within each session, excluding responses made on correction trials. The two Old stimuli (shown in bright blue and bright red) were discriminated with significant accuracy across baseline sessions (these sessions' data are from Experiment 1 and are depicted as an average across stimuli Figure 3.3). When the two New stimuli (shown in dark blue and dark red) are introduced, responding to the New MC resembles responses to the Old MC, while responding to the New MS is markedly less accurate. By the final session of this procedure, discrimination accuracy for all four stimuli is reduced to chance level.

3.4.2 Results: Experiment 2

There was wide variability in the number of sessions needed for the subjects to reacquire the baseline isochronous-triplet discrimination (mean = 16.88; SD=8.56 sessions) (Figure 3.5). Overall, the reacquisition took fewer sessions than previous learning of this discrimination in Experiment 1 (cf. Figure 3.3).

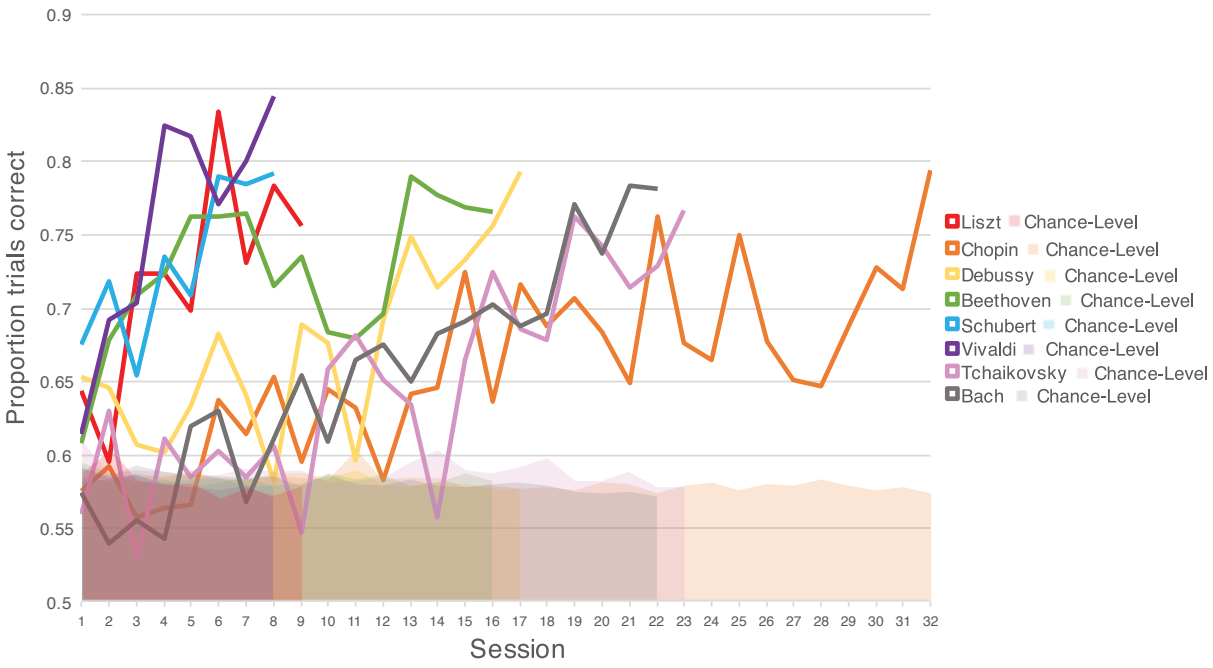

Figure 3.5. Re-acquisition of the isochronous-triplet discrimination used as a baseline in the second experiment. The vertical axis shows the proportion of trials correct excluding correction trials; the horizontal axis shows session number. Lines represent the proportion responses correct for individual subjects across multiple sessions. Chance-level was determined for each session using a binomial test. Shaded areas represent the proportion of correct responses needed to exceed chance-level, for each bird, within each session, determined using a binomial test. Probe trial presentations began immediately after birds met a criterion of 80 percent of trials correct in three sessions.

3.4.2.1 A Strategy Based in Tempo

There was strong agreement between subjects on most of the probe stimuli, indicating that they shared a similar perceptual strategy while performing the discrimination (see Figure 2 in Appendix for between-subjects comparisons). For most of the probe stimuli, the subjects showed a preference to select one response, relating the presented stimulus to whichever baseline pattern was paired with that response key. The data strongly support that the subjects discriminated the stimuli by using the frequency of events, or the overall rate of the patterns. Clear trends emerge in subjects' responses to the faster and slower versions of the baseline patterns, as well as responses to other ratio patterns (Figure 3.6). When an isochronous probe was fast (as in 222222 or 333333) the subjects associated the stimulus with the baseline triplet pattern (226226), ignoring the difference in ratios among intervals in the patterns. When an isochronous probe was slower (as in 999999) the subjects strongly associated the stimulus with the baseline isochronous pattern (666666). This trend also applies to the faster and slower versions of the triplet configuration (113113 and 4-4-12-4-4-12) and to other patterns in which the ratio between intervals was altered.

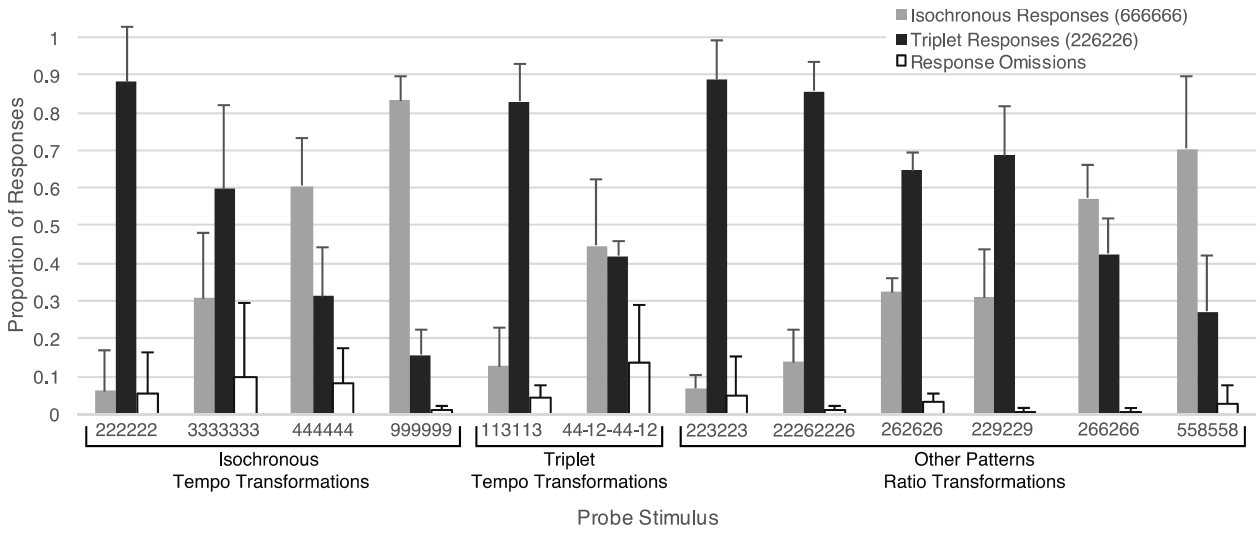

Figure 3.6. Responses made by European starlings towards the equitone probe stimuli presented in Experiment 2. Bars indicate proportion of responses to each probe stimulus averaged across subjects. Error bars show standard deviation. The stimuli are ordered by the average interval length within the pattern, a measure used to approximate tempo, increasing within each stimulus category. The data show the subjects to have discriminated the patterns using the absolute frequency of contained events: stimuli with shorter intervals were associated with the faster baseline triplet 226226 while stimuli with longer intervals were associated with the slower baseline isochronous 666666.

3.5 Discussion

3.5.1 Individual Differences in Performance

The aim of the first experiment, to examine beat perception in starlings, was not met because the birds were unable to learn a basic training discrimination. That all but one subject failed to discriminate between a single MS and MC stimulus was a curious outcome considering that the two patterns, which are both combinations of the same parent set of intervals, could be distinguished easily by attending to the first or final interval, or any subset of consecutive intervals contained within. It was unnecessary for the entire stimulus to be memorized or for an underlying categorical rule to be learned. Anecdotally (and supported by the results of the comparative experiment described in Chapter 2) these two training patterns sound obviously distinct to human listeners. So why, then, did the starlings largely fail to distinguish them? Taken alone, the subjects' failure on the training discrimination might suggest that starlings are insensitive to the global structure of auditory temporal patterns, at least among the equitone stimuli used here. Possible reasons for the subjects' failure to learn to the MS-MC discrimination were explored in the second operant experiment and are discussed further in Chapter 4.

However, one subject, Liszt, was able to learn to consistently discriminate between a single MS and MC stimulus after 40 sessions. The performance of this bird provides limited evidence that starlings are sensitive to some features of these metrical patterns, and that discriminations of equitone stimuli may be learned by starlings with extensive training. In interpreting the large individual differences in discrimination accuracy observed in the MS-MC discrimination, I inferred that the subjects may have used alternate perceptual strategies, either while initially associating each stimulus with a response key, or while listening to the stimuli during subsequent presentations. Based on the high discrimination accuracy that was ultimately

reached by Liszt, I considered that whichever strategy was used by this bird proved the only one effective for consistently discriminating between the two MS-MC stimuli.

When Liszt was tested with two additional MS-MC patterns, a marked drop in accuracy was observed for both of the previously learned stimuli. This decline supports that a stimulus memorization strategy of some kind was used by Liszt, and that the introduction of additional items disrupted retention or retrieval of the associations learned for the previous two stimuli. However, it is worth noting that the "new" MC pattern (14232), which was structurally similar to the "old" MC pattern (23142) in sharing the consecutive intervals 142 and 23, elicited correct responses significantly above chance level almost immediately. After several sessions, Liszt's accuracy on each of the four stimuli dropped to chance level (Figure 3.4). One possible explanation of this result is that Liszt attended towards a single temporal feature, such as a chunked subset of consecutive intervals, that was present in both of the MC stimuli but not in the MS stimuli, and this feature was associated with the right response key rather than the global patterns present in the two MC stimuli (while, conversely, sounds that lacked this feature were associated with the left response key). From this limited data it is impossible to draw conclusions about whatever strategy was used by Liszt, but it is apparent that this strategy was not sufficient to generalize to novel stimuli and support the intended discrimination between the full pool of 44 metric simple and complex patterns.

3.5.2 Characterizing a Perceptual Strategy

The design of the second experiment's probe stimuli considered the strategies that the subjects use. For solving a perceptual problem, do starlings use a strategy based on absolute timing, such as attending to the absolute duration of specific intervals in the patterns? Or, alternatively, are they capable of grasping time in a relational or relative sense, such as recognizing a common pattern presented at a novel tempo? A relational sense of time is considered fundamental to the perception of meter and beat (Hulse et al., 1992; Povel & Essens, 1985; Teki et al., 2011). Yet animal studies have shown that for the most part, other species – including songbirds – exhibit a preference for using absolute frequency of pattern elements in making perceptual judgements (D'Amato & Salmon; Dooling et al., 1987; Hulse et al., 1984). However, under some experimental settings, particularly when absolute timing cues are mitigated, there is evidence to suggest that it is possible for starlings to perceive the relational frequencies of pattern events (Hulse et al., 1990).

Of particular relevance to identifying the use of an absolute or relative timing strategy is the probe 222222, a faster isochronous pattern which shares a common interval with the baseline triplet pattern, but not with the baseline isochronous pattern. If the subjects were attending to the absolute duration of individual intervals in the patterns, I expected they would respond by relating 222222 to the baseline triplet pattern (226226), since they share the interval 2 in common. If the subjects were instead attending to the global pattern of intervals, suggestive of using relative timing, they might respond by relating 222222 to the relatively slower baseline isochronous pattern (666666).

The subjects showed a strong preference to respond to 222222 by pecking the right key, relating its presentation to the baseline triplet pattern 226226. Their responding to this probe

suggests that the birds failed to recognize the presence of isochrony. It also supports that the subjects were timing individual intervals in an absolute sense, since 2 is common to only the baseline triplet pattern. Yet, taken with their responses to the other probe stimuli, it seems more likely that the birds were instead using a strategy based on the perceived rate of the sounds, or the absolute frequency of events, rather than the global structure of the patterns or durations of intervals. In other words, the birds appear to have treated the baseline patterns as triplet-"fast" and isochronous-"slow" and generalized these associations to the novel probe patterns.

Looking to the birds' responses to the other probe stimuli, in which baseline interval ratios have been altered, a strategy based on the overall rate of the sounds fits trends in the data. It might appear superficially that the probe 223223 was recognized by the subjects as a triplet pattern, despite the ratio of intervals within the pattern being closer to isochronous than the baseline triplet (i.e., the difference between 2-3 was less than between 2-6). On the other hand, if the birds were attending to rate of the stimuli rather than the duration of individual intervals, then patterns containing shorter intervals overall might be associated with the relatively faster rate of the triplet baseline pattern. In contrast to 223223, the stimulus 558558 – which more closely resembles the baseline triplet pattern in a relative sense – was apparently matched by the subjects to the baseline isochronous pattern with which it shares longer interval durations. These results are consistent with those of previous behavioural experiments with starlings that show starlings prefer to use absolute temporal information over relations between elements in serial patterns (Comins & Gentner, 2010).

3.6 Chapter Summary

The experiments described in this Chapter have shed light on the perception of auditory temporal patterns by starlings. The first experiment, designed to comparatively test whether starlings are sensitive to regular temporal accents in metrical patterns, was unable to proceed beyond an initial training discrimination. However, by successfully teaching the subjects an alternate discrimination between an isochronous and triplet pattern, I demonstrated that the operant training procedure was effective. From these results I inferred that the birds' inability to learn the previous simple-complex discrimination must be related to their perception of qualities of these stimuli. The second experiment aimed to identify any incompatibility between the design of the equitone stimuli and the perceptual strategies that starlings use for discriminating auditory patterns. Its results suggest that starlings use a strategy that involves attending to absolute timing features, as in the overall rate of the stimuli. Further discussion of these results continues in the second half of Chapter 4 with considerations for future work on rhythm and beat perception in starlings and other animals.

Chapter 3 References

Abe, K., Watanabe, D. (2011). Songbirds possess the spontaneous ability to discriminate syntactic rules. Nature Neuroscience *14*, 1067.

Braaten, R.F., Hulse, S.H. (1993). Perceptual organization of auditory temporal patterns in European starlings (*Sturnus vulgaris*). Perception & Psychophysics *54*, 567–578.

Braaten, R.F., Petzoldt, M., Colbath, A. (2006). Song perception during the sensitive period of song learning in zebra finches (*Taeniopygia guttata*). Journal of Comparative Psychology *120*, 79–88.

Bregman, M.R., Iversen, J.R., Lichman, D., Reinhart, M., Patel, A.D. (2013). A method for testing synchronization to a musical beat in domestic horses (*Equus ferus caballus*). Empirical Musicology Review *7*, 144.

ten Cate, C., Spierings, M., Hubert, J., Honing, H. (2016). Can birds perceive rhythmic patterns? A review and experiments on a songbird and a parrot species. Frontiers in Psychology *7*, 730.

Chakraborty, M., Jarvis, E.D. (2015). Brain evolution by brain pathway duplication. Philosophical Transactions of the Royal Society B: Biological Sciences *370*, 20150056.

Comins, J.A., Gentner, T.Q. (2010). Working memory for patterned sequences of auditory objects in a songbird. Cognition *117*, 38–53.

Comins, J.A., Gentner, T.Q. (2014). Temporal pattern processing in songbirds. Current Opinion in Neurobiology *28*, 179–187.

Cook, P., Rouse, A., Wilson, M., Reichmuth, C. (2013). A California sea lion (*Zalophus californianus*) can keep the beat: motor entrainment to rhythmic auditory stimuli in a non vocal mimic. Journal of Comparative Psychology *127*, 412–427.

D'amato, M. R., Salmon, D. P. (1984). Processing of complex auditory stimuli (tunes) by rats and monkeys (*Cebus apella*). Animal Learning and Behavior *12*, 184-194.

Dooling, R.J., Brown, S.D., Park, T.J., Okanoya, K., Soli, S.D. (1987). Perceptual organization of acoustic stimuli by budgerigars (*Melopsittacus undulatus*): I. Pure tones. Journal of Comparative Psychology *101*, 139–149.

Dooling, R.J., Leek, M.R., Gleich, O., Dent, M.L. (2002). Auditory temporal resolution in birds: discrimination of harmonic complexes. Journal of the Acoustical Society of America *112*, 748–759.

Feare, C. (1984). The starling. Princes Risborough: Shire.

Fitch, W.T. (2006). The biology and evolution of music: a comparative perspective. Cognition *100*, 173–215.

Gentner, T.Q., Hulse, S.H. (2000). Perceptual classification based on the component structure of song in European starlings. The Journal of the Acoustical Society of America *107*, 3369–3381.

Gentner, T.Q., Fenn, K.M., Margoliash, D., Nusbaum, H.C. (2006). Recursive syntactic pattern learning by songbirds. Nature *440*, 1204–1207.

Grahn, J.A. (2012). Neural mechanisms of rhythm perception: current findings and future perspectives. Topics in Cognitive Science *4*, 585–606.

Handel, S. (1993). Listening: an introduction to the perception of auditory events. Cambridge, MA: MIT Press.

Hasegawa, A., Okanoya, K., Hasegawa, T., Seki, Y. (2011). Rhythmic synchronization tapping to an audio–visual metronome in budgerigars. Scientific Reports *1*, 120.

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*, e51369.

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*, 176–196.

Hulse, S.H., Humpal, J., Cynx, J. (1984). Discrimination and generalization of rhythmic and arrhythmic sound patterns by European starlings (*Sturnus vulgaris*). Music Perception *1*, 442–464.

Hulse, S. H., Page, S. C., & Braaten, R. F. (1990). An integrative approach to auditory perception by songbirds. In W. C. Stebbins, M. A. Berkley (Eds.), Wiley series in neuroscience, Vol. 2. Comparative perception, Vol. 2. Complex signals. Oxford, England: John Wiley & Sons. pp. 3-34.

Hulse, S.H., Takeuchi, A.H., Braaten, R.F. (1992). Perceptual invariances in the comparative psychology of music. Music Perception *10*, 151–184.

Itatani, N., Klump, G.M. (2011). Neural correlates of auditory streaming of harmonic complex sounds with different phase relations in the songbird forebrain. Journal of Neurophysiology *105*, 188–199.

Jarvis, E.D. (2007). Neural systems for vocal learning in birds and humans: a synopsis. Journal of Ornithology *148*, 35–44.

Maier, E.H., Klump, G.M. (1990). Auditory duration discrimination in the European starling (*Sturnus vulgaris*). The Journal of the Acoustical Society of America *88*, 616–621.

MacDougall-Shackleton, S.A., Hulse, S.H., Gentner, T.Q., White, W. (1998). Auditory scene analysis by European starlings (*Sturnus vulgaris*): perceptual segregation of tone sequences. Journal of the Acoustical Society of America *103*, 3581–3587.

McAuley, J.D. (2010). Tempo and rhythm. In M.R. Jones, R.R. Fay, A.N. Popper (Eds.), Music Perception. New York, NY: Springer New York, pp. 165–199.

McDermott, J.H., Hauser, M.D. (2005). The origins of music: innateness, uniqueness, and evolution. Music Perception *23*, 29–59.

Mountjoy, J.D., Lemon, R.E. (1995). Extended song learning in wild European starlings. Animal Behaviour *49*, 357–366.

Patel, A.D. (2006). Musical rhythm, linguistic rhythm, and human evolution. Music Perception *24*, 99–104.

Patel, A.D., Demorest, S.M. (2013). Comparative music cognition: cross-species and cross-cultural studies. In D. Deutch (Ed.), The Psychology of Music *3*. San Diego: Academic Press. pp. 647–681.

Patel, A.D., Iversen, J.R., Bregman, M.R., Schulz, I. (2009). Experimental evidence for synchronization to a musical beat in a nonhuman animal. Current Biology *19*, 827–830.

Pavlova, D., Pinxten, R., Eens, M. (2005). Female song in European starlings: sex differences, complexity and composition. The Condor *107*, 559–569.

Povel, D.J., Essens, P. (1985). Perception of temporal patterns. Music Perception *2*, 411–440.

Schachner, A., Brady, T.F., Pepperberg, I.M., Hauser, M.D. (2009). Spontaneous motor entrainment to music in multiple vocal mimicking species. Current Biology *19*, 831–836.

Slater, P. (1983). Bird song learning: theme and variations. Perspectives in Ornithology: Essays Presented for the Centennial of the American Ornithologists' Union *475*.

Teki, S., Grube, M., Kumar, S., Griffiths, T.D. (2011). Distinct neural substrates of duration-based and beat-based auditory timing. Journal of Neuroscience *31*, 3805–3812.

van der Aa, J., Honing, H., ten Cate, C. (2015). The perception of regularity in an isochronous stimulus in zebra finches (*Taeniopygia guttata*) and humans. Behavioural Processes *115*, 37–45.

Zarco, W., Merchant, H., Prado, L., Mendez, J.C. (2009). Subsecond timing in primates: comparison of interval production between human subjects and rhesus monkeys. Journal of Neurophysiology *102*, 3191–3202.

Chapter 4

4.0 Summary of Results

In the previous two chapters I aimed to compare between humans and songbirds the capacity to perceive a beat in auditory rhythms that I created based on the Povel and Essens (1985) clock-induction model. Using a novel testing paradigm, I conducted a series of behavioural experiments in which human participants and European starlings (*Sturnus vulgaris*) were trained to discriminate between metric simple (MS) and metric complex (MC) patterns. These metrical categories could distinguished by whether or not regular temporal accents were detected while listening to a stimulus. The humans were able to learn this task even with only implicit instructions, and musical expertise significantly predicted their accuracy on the discrimination. The starlings, in contrast, failed to reach an accuracy criterion in their responding to advance beyond the initial training procedure, a discrimination between only two patterns, and the comparative experiment was thus unable to proceed. A second operant experiment probed starlings' perception of temporal patterns more generally, revealing that the birds attend to overall rate or the absolute frequency of sound events. In this chapter I critically discuss the design and results of these experiments.

4.1 Experiments with Human Participants

4.1.1 Use of Cognitive Strategies

Immediately following the generalization task, human participants completed a debrief questionnaire in which they provided demographic information about their musical experience and ability, as well as reports of their attention, confidence and deliberate use of a strategy during the experiment (see Tables 4.1 and 4.2 below). Some reported to have relied on memorizing or mentally reproducing the patterns, which previous investigations have shown to influence beat perception (Essens & Povel, 1985; Grahn & Brett, 2007; Patel et al., 2005).

Table 4.1. Strategies reported on the debrief questionnaire by human participants (n = 39) in the explicit instructions experiment, in which subjects were provided with a definition of beat as part of the task instructions. The two response options were labelled as “stronger beat” and “weaker beat”. Columns 1 and 2 show responses to two items from the debrief questionnaire: a rating of the proportion of responses for which the participant was uncertain, and their response indicating whether they had or had not moved along to the sounds during the task. Column 3 lists the three bins of participants’ scores on the Beat Expertise factor as a measure of their musical skill. Column 4 lists percent generalization trials correct for each participant in increasing order (accuracy on the training is excluded). Column 5 lists all strategies reported by participants. Those who did not report using any strategy are not shown.

Explicit Instructions

1 Uncertain (1=never, 10=always)	2 Moved during task?	3 Beat Expertise	4 Generaliz. Accuracy ▼	5 Reported Strategy (as written)
2	No	Intermediate	50%	Closing my eyes to visualize beat
4	No	Novice	53%	The beats that felt like they could be used in an upbeat song were usually strong beats
7	Yes	Novice	57%	Tap to the beat
7	Yes	Novice	57%	I searched on Google at the beginning, how to recognize strong beat & weak beat
6	No	Novice	58%	Imagining the sound in the background of a song, then determining if I liked the song. Also memorizing if specific sounds were correct/incorrect.
4	No	Intermediate	58%	listening or patterns in gaps or rhythms between beeps
8	Yes	Novice	61%	Using the gaps between each tone to determine the category
10	No	Novice	62%	None worked - tried counting beats; irregular vs regular ending on even vs odd beats
7	Yes	Expert	63%	Weaker beat = less spaces between the tones
8	No	Novice	64%	I learned to listen carefully to pauses during the sounds, which seemed to be associated with "weak" beats
4	Yes	Novice	71%	Tried to relate back to musical time signature. Tried to find beats that were consistent - they were usually strong beats
2	Yes	Intermediate	71%	When the beat was weak, there were more off-beats or pauses
5	Yes	*Missing data*	73%	I recognized some of the same beats
4	Yes	Expert	80%	I tried to listen to the downbeats
3	No	Intermediate	81%	They didn't really work but counting out a 4-beat pattern helped
1	No	Intermediate	82%	Break it down into its smallest time increments and count them there. Look for off beat endings
3	Yes	Intermediate	83%	When I heard the sound for the first time, if I could remember the beats, I thought it was a strong sense of beat
3	Yes	Expert	86%	I tried to see if it could be repeated and make a coherent pattern. Tap along to it easily = strong beat
4	No	Intermediate	88%	Spacing between sounds were equal for the majority of the piece (per set of beats)
1	No	Expert	88%	I correlated offbeats to a weaker beat
2	No	Expert	89%	Replacing skips in the beat in my head for timing
3	Yes	Expert	91%	When the first half of the beat played I tried to finish off what the rest should sound like in my head, and if what played matched with my expectation, I would then click strong and vice versa
3	No	Novice	92%	I pretended I was tapping my feet
3	Yes	Intermediate	96%	If a sound fell on the off beat, it was weak. When sounds were on the on beat, they were strong
1	Yes	Expert	98%	Counting the strong beats in my head up to 4

Table 4.2. Strategies reported on the debrief questionnaire by human participants (n = 38) in the implicit instructions experiment, in which the discrimination rule was ambiguous. The two response options were identified as “Category A” (for metric simple) and “Category B” (for metric complex). Column 1 and 2 show responses to two items from the debrief questionnaire: a rating of the proportion of responses for which the participant was uncertain, and a response indicating whether they had or had not moved along to the sounds during the task. Column 3 lists the three bins of participants’ scores on the Beat Expertise factor as a measure of their musical skill. Column 4 lists percent generalization trials correct for each participant in increasing order (accuracy on the training is excluded). Column 5 lists strategies reported by participants. Those who did not report using any strategy are not shown.

Implicit Instructions

1 Uncertain (1=never, 10=always)	2 Moved during task?	3 Beat Expertise	4 Generaliz. Accuracy ▼	5 Reported Strategy (as written)
6	Yes	Intermediate	43%	Visualize, count in my head
4	No	Novice	48%	I checked if the last beat was singular or if it followed several quick beats
7	No	Intermediate	51%	If there were eighths vs quarters, location of the eighths changed as we progressed
6	Yes	Novice	52%	Tried to use the responses in the previous questions to find a pattern and see which sound was which
6	No	Novice	56%	Even number of beats - A. Odd - B
7	No	Expert	60%	I tried to count it out in my head and apply musical knowledge
5	Yes	Novice	61%	"Group number of beats"
8	No	Intermediate	66%	I account the space between the sound
6	Yes	Intermediate	69%	I would count the beats out in my head to see if there was proper rhythm
8	Yes	Expert	69%	Each one had a different beat/tempo.
6	Yes	Intermediate	69%	Tried to see which patterns had more off beats
8	No	Intermediate	69%	I tried counting the beeps @ the beginning and end and trying to find the similarities
6	Yes	Intermediate	70%	I counted the amount of sounds I heard. "A = shorter, B = longer, quicker. Counting over 7 sounds = B"
6	Yes	Expert	71%	Category A: * *** * or **** ** Category B: ** ** ***
6	Yes	Novice	73%	Some had a good beat vs those that didn't
6	No	Expert	73%	I tried grouping the sounds into beats (beats of 4, 5, 6, etc). I looked for uneven patterns versus straight sounds. The timing between sounds (if it's evenly divided or if some sounds came early or late)
4	No	Intermediate	73%	Noticing rhythm patterns
2	Yes	Intermediate	74%	Number As have repeating sounds
5	Yes	Intermediate	74%	1 or 3 beats in a row = A, 2 beats in a row = B, didn’t always work
2	Yes	Novice	76%	The sounds in category 1 sound more consistent
5	No	Novice	78%	Group a had 1 beep at the beginning + group B had 2 fast beeps at the beginning
3	Yes	Novice	78%	Has a improvement in distinguishing sounds
3	No	Expert	79%	Counting musically (1 and 2 and 3 and 4) or in triplets
3	No	Intermediate	79%	Cat A sounded "right", Cat B sounded "off"
4	Yes	Intermediate	81%	Remembered the rhythm of a category A that I knew was correct and compared other sounds to it
3	Yes	Expert	83%	Counting the number of beats. Trying to figure out the number of times the tempo changed
2	Yes	Expert	83%	In the first example of Category B there were two fast notes, so everytime I hear the two notes together in the beginning, I know its category B. I think there were also some on-beat and off-beat difference but I wasn't really sure
3	Yes	Expert	86%	Category A sounded a little like a christmas tune so I would sing it in my head
4	Yes	*Missing data*	93%	Category A is some dots with rhythms but category B not
2	Yes	Intermediate	95%	Counted in slow 4/4 time --> syncopated/unsyncopated -> either fell on strong beats or on weak 16th beats
2	No	Novice	96%	Count beats in my head
1	Yes	Expert	97%	Listen for the four main beats if they were there. "A = on the beat, B = off the beat"

In both the explicit and implicit experiments there were large individual differences in accuracy. When participants were explicitly instructed to discriminate based on beat strength, some were unable to do so consistently. The relatively low discrimination accuracy of these participants throughout the training and generalization might be suggestive of poor beat perception ability. The significant correlations between accuracy and scores on the Beat Alignment Test support this conclusion. In the implicit instructions condition, the observed low accuracy of some participants might also indicate that they simply never figured out the rule underlying the discrimination, and this could be reflected in the strategies that they reported.

Even with the poor performance of some implicitly instructed participants, the high discrimination accuracy of other participants provides evidence that humans can spontaneously find a beat in these stimuli even without prior expectations of a beat. This was critical to determine for the intended comparison with songbirds and the potential utility of this paradigm for further comparative studies. Since other species are incapable of being explicitly instructed, operant methods require that non-human animals learn the discrimination using only reinforcement as feedback.

It is interesting to consider what prior information the participants may have used to solve the discrimination, and this may be reflected in the diverse range of strategies reported on the debrief questionnaire. Though it is inevitable that any tested adults will have some familiarity with music, those who have received training on music theory may have an advanced comprehension and appreciation of metrical structure. A total of fourteen participants, approximately one third of those who received implicit instructions, described using the beat in their strategy, even though beat was never mentioned to them. At some point in the experiment these participants spontaneously became aware that the beat was relevant to the discrimination

and developed expectations of finding a beat on subsequent trials. This moment of realization – a transition from implicit to explicit awareness of a beat – may coincide with a shift between exogenous (bottom-up) and endogenous (top-down) systems for temporal orienting of attention. Further research on involvement of these systems in beat perception could use a version of the implicit discrimination in combination with neuroimaging techniques to compare brain activation in states of implicit and explicit awareness of beat (as in Coull & Nobre, 2008).

However, it is worth noting that beat is a term often used colloquially in descriptions of music, and it may hold alternate meanings particularly among musical non-experts. The strategies that were reported by implicitly-instructed participants should be interpreted accordingly, since no definition of beat was provided to them. Apart from individuals' reported number of years of past musical training as well as the format of their training, the scope of the participants' previous knowledge of beat or metrical structure is unknown. In future research on implicit awareness of beat it may be valuable to obtain a measure of participants' understanding of these concepts before the task, perhaps by quizzing them on a pre-screening questionnaire.

4.1.2 Use of Motor Synchronization

This discrimination paradigm is concerned with beat perception and not beat production, and to divorce the two requires that the subject refrains from synchronizing their movement to auditory stimuli. Entrainment of body movement may make it easier to find a beat (Su & Pöppel, 2012). I expected that moving along to the stimuli might improve subjects' accuracy in classifying the metric simple patterns, while also increasing their chances of finding a beat in metric complex patterns (thus increasing incorrect responses). In both the explicit and implicit instructions all participants were told to refrain from moving during the task, so as to reduce the

likelihood that tapping a finger or bouncing a foot might provide some external regular cue apart from the accents that emerge in the stimuli.

But evidently, simply asking the participant to remain still was not enough: according to their responses on the debrief questionnaire approximately half indicated they did move along to the stimuli despite the instructions. It is possible that some additional subjects to these were reluctant to admit to disobeying the instructions and that this proportion is underestimated. From this simple questionnaire data alone it is unclear when, over the course of the experimental session, the participants began synchronizing their movement to the stimuli. It is also unknown to what features of the stimuli they synchronized their movement. An altered version of this paradigm could examine the effects of motor synchronization on discrimination performance by incorporating the tendency of humans to move along to the stimuli, perhaps by recording their movement during the task using motion capture technology.

4.2 Limitations

4.2.1 Single-Session Testing

The results of these experiments provide strong evidence that human participants with more musical expertise were better at this discrimination than non-experts, consistent with findings of previous rhythm experiments (Bouwer et al., 2018; Cameron & Grahn, 2014; Grahn & McAuley, 2009). From these data it is tempting to conclude that musicians are better at beat perception. However, it is also important to consider that musical experts may have approached the task differently than non-experts, perhaps with greater determination or confidence in their ability, and these differences may also contribute to the significant effect of musical expertise that was observed. The significant correlation between accuracy on the generalization and scores on the Beat Alignment Test (BAT) suggests that this discrimination task measures participants'

ability to detect auditory beat. But it is possible that performance of both the experimental discrimination and the BAT within a single testing session may have been jointly impacted by the subject's attention, motivation or other aspects of their mental state at the time. If data were collected and averaged across multiple test sessions, these variables may be accounted for. Multiple testing sessions would also create a wider window for further examination of subjects' learning across prolonged exposure to the stimuli and would improve equivalence with multi-session operant training of animal subjects on this discrimination.

4.2.2 Metrical Stimulus Design

The metric simple and metric complex stimuli were created and divided into discrete categories based on only a single type of metrical structure, one that contained perceptual groups of onsets spanning four units. The Povel & Essens model predicts that the simple patterns would best fit with a 4-unit clock, while the complex patterns would not fit well. The design of these stimuli in keeping with a 4-unit clock follows the methodology of previous studies that have used simple and complex patterns (Cameron & Grahn, 2014; Grahn & Brett, 2007). These experiments did not test humans' perception of other possible meters.

4.3 Operant Experiments with Starlings

Though previous studies have offered ideas of how songbirds process auditory rhythmicity, little research has directly looked at sensitivity to beat in this taxonomic group. In the first operant experiment I presented auditory rhythms that were created based on the Povel & Essens clock-induction model. This experiment tested whether starlings, a species of songbird, can perceive regular temporal accents and use their perception of accent structure to discriminate auditory rhythms (Povel & Essens, 1985). The categorization paradigm I developed provides a means to examine beat perception in a non-human animal without requiring the subject to synchronize its movement. Standardization of this methodology may potentially enable direct comparisons of beat perception across other species.

The aim of the first operant experiment was to examine beat perception in songbirds. This aim was not met due to unexpected incompatibility between the auditory stimuli and test species. The starling subjects failed to discriminate between a single metric simple and metric complex pattern, both permuted from the same set of intervals. I therefore conducted a second operant experiment to diagnose this failure and identify the temporal features of these stimuli that the birds were sensitive to. The results of the second experiment are consistent with findings of previous experiments reported in the literature that show starlings and other songbirds to be sensitive to the absolute frequency of temporal events (Braaten & Hulse, 1993; Dooling et al., 1987; Hulse et al., 1990). The results also explain their earlier failure on the simple-complex discrimination. If the birds attended to some temporal aspect of the stimuli based in absolute timing, such as the overall rate or the absolute frequency of sound events, then the two metrical training patterns, which shared identical intervals, would be perceptually indistinguishable. In contrast, the isochronous and triplet patterns could be distinguished easily on the basis of

absolute timing (the latter being faster) and a discrimination between these two stimuli was learned by the subjects relatively quickly. This insight into starlings' use of absolute timing contributes information towards designing appropriate metrical or beat-based stimuli for presenting to this species in future experiments. Knowing that absolute timing is the default strategy recruited by starlings for these kinds of auditory discriminations, it may be worthwhile to first train subjects on simpler rhythm discriminations in order to teach them to pay attention to relative timing cues. Once the use of relative timing is established, the subject may only then advance to the beat-based discrimination task described here.

4.3.1 Comparative Assumptions

A series of experiments by Hulse, et al. found that starlings are capable of discriminating rhythmic from arrhythmic auditory patterns under specific experimental settings (Hulse et al., 1984). The notion that songbirds are capable of learning abstract concepts based in relative timing (e.g., regularity, or relative relations between intervals) that are sufficiently robust to be generalized across novel tempi has been proposed by some authors but remains unsubstantiated (van der Aa et al., 2015; Hulse et al., 1984). In most of the previous work that has examined the perception of temporal patterns by songbirds, regularity is physically manifested in auditory stimuli, including but not limited to isochronous metronomic patterns. The paradigm I describe in this thesis requires subjects to instead attend to an internal regularity – the sense of pulse that may arise from the perception of regular temporal accents.

However, the sensitivity of songbirds to accents in sound is unclear, and it is not known whether other animals perceptually derive accents from the temporal properties of auditory patterns, as has been modelled in humans. For the present simple-complex discrimination to be learned, the subject would need to be able to perceive temporal accents, and so a critical, but

perhaps unfair, assumption about songbirds' sensitivity to accents was made in recruiting starlings for this study. Establishing whether other species perceive accents, including those that arise from the temporal properties of rhythm, is an important topic for future exploratory experiments. It may be possible that other species are sensitive to regularities in certain types of accents but not others. One recent study compared behavioural responses of zebra finches (songbirds) and budgerigars (parrots) to auditory rhythms that contained accents produced with slight variations in intensity of certain tones that were presented at a different frequency from the standard tone (ten Cate et al., 2016). They found no evidence for perceptual grouping or pulse perception. The current experiment can be differentiated from this work by its exclusive use of identical tones and focus on temporal accents, rather than intensity accents. One way this research could be further pursued is by adapting methods used previously to study accent perception in humans, such as tasking the subject with adjusting the volume of a presented tone to match the perceived intensity of an accented note (Povel & Okkerman, 1981). In establishing if or how individual accents are perceived by other animals, this information may contribute towards the design of more appropriate rhythmic stimuli for testing the perception of accent structure and beat.

Humans that are enculturated with Western music are thought to initially expect auditory rhythms to fit with duple meter, since this is the most common metrical structure (Vuust & Witek, 2014; van der Weij et al., 2017). Listeners will predict future accented events to align in time with a duple beat (Grahn & Rowe, 2013). Many experimental studies of beat have followed the Povel & Essens model for designing rhythms in which regular perceived accents align with a metrical 4-clock (Grube & Griffiths, 2009; Shmulevich & Povel, 2000; Shu-Jen et al., 2013). Yet a number of other metrical structures exist that were not considered in this thesis. For example,

triple meter, in which the basic unit consists of three beats, is also common in Western music (Randel & Apel, 1986). The equitone stimuli used in the comparative experiments were divided into two categories based on the contained patterns' counterevidence score against a 4-clock, keeping with the category boundaries for metric simple and metric complex used in other work. In presenting these stimuli to songbirds it was assumed that the test species would also be sensitive to this metrical structure. However, the applicability of clock-induction models to temporal processing in other species has not been established. Future comparative investigations that use such models should consider probing the sensitivity of other species to metrical structures outside of those preferred by humans, and may wish to incorporate alternate meters, such as a 3 or 5-unit clock, in designing stimuli that will elicit regular accents.

I constructed all of the stimuli for the operant experiments with sinusoidal tones presented at a frequency and at rates that I selected through an ecological approach of analyzing birdsong. However, I could only assume that these parameters were appropriate for the birds' perceptual sensitivities. The response data says little about how these properties were subjectively received by the starlings, and there is little discussion in the literature of what starlings prefer in sounds outside of conspecific song. The range of rates that starlings are sensitive to in auditory patterns remains undefined and warrants further study. Other investigations of pattern learning in this species have used faster rates, and some have claimed their stimuli to be ecologically valid by incorporating recorded elements of starling vocalizations (Braaten & Hulse, 1993; Comins & Gentner, 2010; Comins & Gentner, 2014). It seems plausible that the rate of the stimuli used in this thesis may have been too slow for starlings to perceive any patterns that span multiple events. Theoretically, if starlings use a perceptual sliding window of some kind to aid in encoding the timing of a sequence of events, it may be that the rate of the

equitone stimuli used here exceeded the relatively narrow temporal boundaries of this window. Humans are sensitive to beat in auditory rhythms only within a specific range of tempi; it is possible that this range might be species-specific. It would be worthwhile to retry the simple-complex discrimination with starlings using the same metrical patterns, but this time presented at a faster rate and perhaps constructed with other sounds instead of pure tones (e.g., clicks, as in starling vocalizations).

4.3.2 Methodological Considerations

The three pilot subjects failed to initially discriminate between a single metric simple and metric complex pattern, and subsequently all but one of the subjects failed to learn the experimental simple-complex discrimination. Why were these birds unable to learn a seemingly easy training task, even with thousands of trials' worth of response feedback? To reach above-chance discrimination accuracy, subjects could have solved this task in multiple simple ways. For example, the patterns could be easily distinguished by attending to the first or last interval, both of which differed between the two. As I combed the literature for information on starlings' perception of temporal patterns, it occurred to me that maybe the birds were applying a perceptual strategy that wasn't compatible with this discrimination in particular but that starlings use as a general framework for auditory timing. It is possible that at some point in the experiment the birds developed their strategy for discriminating between two stimuli, and then maintained this strategy throughout subsequent transfers to novel stimuli. Between the first and second operant experiments the birds underwent multiple transfers between discriminating the isochronous-triplet and the MS-MC patterns. Counterbalancing the order of transfers between the discriminations could have controlled for the perseveration of a strategy.

The first operant experiment required subjects to learn associations for two response options: if regular accents were detected, respond “left”, and if no accents were detected, respond “right”. In the explicit experiment with human subjects, these responses were labelled “stronger beat” and “weaker beat”. However, the testing procedure could have instead been structured in a simpler manner such that only a single response option is needed. For instance, in a Go/No-Go configuration of this task (as used successfully by ten Cate et al., 2016 for a similar experiment) the subjects could be taught to selectively respond only when regular temporal accents are perceived, and to withhold responding when accents are irregular or absent. This reduced procedure might be easier for an animal subject to learn relative to categorization choice task.

The starlings tended to repeatedly peck at the response keys throughout each trial until reinforcement was delivered. In at least one previous study of starlings’ perception of temporal patterns, the subjects were successfully trained to delay responding for up to 25 seconds until the offset of prolonged auditory presentations (Braaten & Hulse, 1993). This required extensive, gradual shaping of the response behaviour. Since auditory beat is a percept that arises over time, I reasoned that it was important for the subjects to listen to the entire stimulus before making a judgement. I initially attempted to train the starlings to delay responding using a similar shaping procedure to that described by Braaten & Hulse 1993, such that premature pecks recorded earlier than a specified delay (of incrementally increasing duration) would result in the lights turning off. The birds were to learn to delay pecking one of the response keys until after the full length of a stimulus (7 seconds) had elapsed.

After several weeks of training, the pilot subjects were unable to learn to withhold pecking during stimulus presentations, even for a delay of only two seconds. In lieu of requiring the subject to withhold responding, I modified the procedure such that only the first peck

registered after stimulus offset would produce feedback, thereby extending the mandatory length of exposure to each stimulus before responding and keeping with delay procedures used in other operant experiments with starlings (Gentner and Hulse, 2000). Still, the tendency of starlings to unremittingly peck at the response keys is problematic, and it is unclear to what extent a subject will actively perceive a stimulus during the behaviour. To satisfy this tendency, future work might consider inserting an additional inert key that the bird may peck repeatedly to no effect, but then require the bird to transfer their pecking to the response key(s) after a stimulus presentation ends. Or, the birds could be trained to start trials and remain perched some distance from the response keys until the stimulus ends. Additionally, the use of autoshaping procedures may also be effective for teaching the delay using a secondary reinforcer, such as illuminating the keys during the allotted window for inputting responses.

Relative to the few other vocal learning animal groups (e.g., bats, elephants, cetaceans, seals, hummingbirds, parrots) songbirds are accessible and highly suited for behavioural research. Many authors that have applied operant methods with wild-caught songbirds have achieved good success. Yet, what is easy to overlook is that studies often use birds with individual histories of previous experimental training. In general, operant behavioural testing requires that a test subject lives for many months in captivity, during which they may become habituated to their environment and familiar with humans.

The use of mature, recently-caught wild starlings in this thesis presented a number of challenges for animal husbandry and the experiments. I began training the pilot subjects only nine weeks following their capture and the rest of the birds a few weeks thereafter. The starlings' behaviour in captivity was often unpredictable. For instance, several subjects learned to manipulate the food hopper while inside the testing apparatus such that they could access food

rewards without performing trials. One bird developed a knack for wetting the entire box using the provided water bottle resulting in recurrent hardware damage. Another bird extinguished responding on numerous occasions due to the keys becoming (seemingly deliberately) clogged with food debris. Four of the birds discovered that they could pry open the doors to their individual home cages, and when left unsupervised, would escape into the room, break open containers and effectively undo their caloric restriction. These and other incidents contributed significant delays to data collection.

I also considered how the birds' training may have been impacted by stress. Initially, some of the starlings required several sessions to habituate to the testing environment and the presence of humans before responding. Sessions took place in a separate room away from the birds' home cages, which necessitated that each subject was transferred to and from the testing apparatus daily by the experimenter. This process was met with considerable resistance from some of the birds. Once inside the relatively small, dimly-lit boxes, the birds were individually confined for two hours in silence (apart from the tonal stimuli). Throughout the data collection period some subjects would typically stop responding altogether within a few minutes of the end of each session, despite maintaining an appetite. When the experimenter returned after exactly two hours, the birds would often appear to be waiting in anticipation and many displayed stereotypic flipping behaviors inside the boxes. My impression was that the birds were routinely stressed by their predictable interactions with humans, although after three months at least half did habituate to the transfers between rooms.

An alternative approach that reduces these interactions is to have the subjects live inside the testing apparatus, thereby creating a closed economy (e.g., Bregman et al., 2016; Weisman et al., 1998). For behavioural experiments with captive wild birds, this configuration may be more

practical for collecting data across a large number of trials. Starlings being large and very messy animals means that a closed economy for both housing and testing them would require a larger containment area than the current operant boxes afford. An additional, perhaps more time-consuming method for circumventing certain undesirable traits of wild adult starlings would be to rear juvenile starlings in captivity, so as to habituate them to handling by experimenters and the behavioural testing procedures well in advance of data collection.

4.4 Future Directions

4.4.1 Rhythm Development in Non-Humans

Should testing of other species' capacities for rhythm find that adult non-human animals cannot perceive an auditory beat or metrical structure in general, it may still be theoretically possible for younger animals to learn. The vocal learning hypothesis proposes that auditory-motor neural networks used by certain animals for vocal learning enables them to perceive a beat and synchronize motor behaviour to a beat (Patel, 2006). In this thesis I examined the sensitivity of adult songbirds to auditory beat in order to test this hypothesis. One interpretation of the vocal learning hypothesis suggests that the developmental process of vocal learning predisposes animals to certain early experiences that are necessary for the cognitive mechanisms underlying beat perception to manifest. By this theory, the relationship between vocal learning and beat perception ability may be one that emerges in the development and life experiences of an animal, and vocal learning as a trait may not be wholly sufficient for beat perception ability to arise (Schachner, 2013). Apparently, beat perception ability may occur in animals independent of vocal learning; this experiential interpretation of the hypothesis partly explains the incidence of motor entrainment to beat in vocal non-learning species, such as pilot data demonstrating synchronization of gait in a dressage horse (Bregman et al., 2013) and the finding that a young

captive California sea lion learned to accurately synchronize its head bobbing to the beat of music with intensive shaping and training (Cook et al., 2013). In such cases, the life trajectory of the animal has been irrevocably altered by interactions with humans starting from a young age. This interpretation may also explain why, considering entrainment ability has been shown in some captive parrots (that are exposed to music and cues provided by humans) movement in synchrony with rhythmic sound is not observed in all parrots.

Studies with human infants have found evidence to support the existence of a sensitive period for rhythm early in development, during which one's perception of metrical structure may be shaped by musical experiences (Hannon and Trehub, 2005). Sensitive and critical periods for vocal learning also exist in other groups of animals. The contributions of phylogenetic, neural and molecular factors to the development of vocal learning have been examined in multiple species (Gahr, 2000; Webb and Zhang, 2005) but the greatest attention has been given to songbirds as a model of human speech development (Brenowitz and Beecher, 2005; Goldstein et al., 2003; Kuhl, 2003). The acquisition of speech by humans and of species-typical vocalizations by songbirds share both parallels and differences (reviewed by Wilbrecht and Fernando, 2003). In light of these comparisons, it is possible that an early sensitive period for rhythm development may also occur in songbirds. Perhaps only with exposure to specific auditory regularities introduced early in life (and in the case of non-humans, with appropriate training) can sensitivity to metrical rhythm or beat be cultivated in animals. To test if this holds true, the capacity of juvenile songbird subjects to learn to respond to accents or beat should be explored further. However, it is important to consider the ecological validity of any result obtained from an non-human animal subject that is reared and trained by humans, and other authors have raised concerns over the interpretation of behavioural data from artificial laboratory-based testing

(Hoeschele et al., 2015). From an ethological perspective, demonstrating the capacity of an animal subject to learn to behave in a certain manner says little about what is typical of the behaviour of the species.

4.5 Concluding Statement

In this thesis I have developed a novel paradigm for testing if the capacity to perceive an auditory beat exists in non-human animals. I also applied the paradigm to test implicit awareness of a beat in humans. In the introduction Chapter I outlined three objectives, two of which were ultimately met. The first – to confirm that the discrimination task captures beat perception ability – was achieved in finding a positive relationship between performance and scores on the Beat Expertise index. A second objective was to determine whether humans can be made implicitly aware of a beat in these auditory rhythms. The implicit instructions experiment revealed that humans will detect regularity in accent structure even when not expecting to find a beat, an important result considering the inability of other species to be verbally instructed on the requirements of this task. The third objective – to test the capacity of starlings to perceive auditory beat – was not met. The comparative operant experiment could not proceed as planned because the subjects failed to acquire the first training discrimination between two patterns. A second operant experiment was conducted aiming to diagnose subjects' failure to learn the initial comparative discrimination. I found that the starlings used a tempo-based perceptual strategy that is consistent with results of previous investigations of auditory discrimination learning in this species. Further work is needed to test a prediction of the vocal learning hypothesis that songbirds have the capacity to perceive auditory beat, and more fundamentally, to determine whether other species perceive temporal accents in sounds.

In future research on these topics, particularly with bird species that are phylogenetically distant from humans, care must be taken to avoid making anthropomorphic assumptions about the sensitivities of other animals in the design and presentation of auditory rhythms. Comparative studies are valuable for exploring commonalities in auditory processing across species, but the uniqueness of human musicality and variation among the perceptual systems of non-humans must not be discounted. In this instance, starlings' bias to use absolute timing presents a challenge for creating suitable stimuli for testing their rhythmic capacities and for comparing their use of temporal information with that of humans. Nonetheless, starlings and other songbirds offer promising models of auditory processes in vocal learning species that may prove useful for further research of how humans and other animals perceive rhythm, accents and beat.

Chapter 4 References

Bouwer, F.L., Burgoyne, J.A., Odijk, D., Honing, H., Grahn, J.A. (2018). What makes a rhythm complex? The influence of musical training and accent type on beat perception. PLoS One *13*, e0190322.

Braaten, R.F., Hulse, S.H. (1993). Perceptual organization of auditory temporal patterns in European starlings (*Sturnus vulgaris*). Perception & Psychophysics *54*, 567–578.

Bregman, M.R., Iversen, J.R., Lichman, D., Reinhart, M., Patel, A.D. (2013). A method for testing synchronization to a musical beat in domestic horses (*Equus ferus caballus*). Empirical Musicology Review *7*, 144.

Bregman, M.R., Patel, A.D., Gentner, T.Q. (2016). Songbirds use spectral shape, not pitch, for sound pattern recognition. Proceedings of the National Academy of Sciences *113*, 1666–1671.

Brenowitz, E.A., Beecher, M.D. (2005). Song learning in birds: diversity and plasticity, opportunities and challenges. Trends in Neurosciences *28*, 127–132.

Cameron, D.J., Grahn, J.A. (2014). Enhanced timing abilities in percussionists generalize to rhythms without a musical beat. Frontiers in Human Neuroscience *8*, 1003.

Comins, J.A., Gentner, T.Q. (2010). Working memory for patterned sequences of auditory objects in a songbird. Cognition *117*, 38–53.

Comins, J.A., and Gentner, T.Q. (2014). Auditory temporal pattern learning by songbirds using maximal stimulus diversity and minimal repetition. Animal Cognition *17*, 1023–1030.

Cook, P., Rouse, A., Wilson, M., Reichmuth, C. (2013). A California sea lion (*Zalophus californianus*) can keep the beat: motor entrainment to rhythmic auditory stimuli in a non vocal mimic. Journal of Comparative Psychology *127*, 412–427.

Coull, J., Nobre, A. (2008). Dissociating explicit timing from temporal expectation with fMRI. Current Opinion in Neurobiology *18*, 137–144.

Dooling, R.J., Brown, S.D., Park, T.J., Okanoya, K., Soli, S.D. (1987). Perceptual organization of acoustic stimuli by budgerigars (*Melopsittacus undulatus*): I. Pure tones. Journal of Comparative Psychology *101*, 139–149.

Essens, P.J., Povel, D.J. (1985). Metrical and nonmetrical representations of temporal patterns. Perception & Psychophysics *37*, 1–7.

Gahr, M. (2000). Neural song control system of hummingbirds: comparison to swifts, vocal learning (songbirds) and nonlearning (suboscines) passerines, and vocal learning (budgerigars) and nonlearning (dove, owl, gull, quail, chicken) nonpasserines. Journal of Comparative Neurology *426*, 182–196.

Gentner, T.Q., Hulse, S.H. (2000). Perceptual classification based on the component structure of song in European starlings. The Journal of the Acoustical Society of America *107*, 3369–3381.

Goldstein, M.H., King, A.P., West, M.J. (2003). Social interaction shapes babbling: testing parallels between birdsong and speech. Proceedings of the National Academy of Sciences *100*, 8030–8035.

Grahn, J.A., Brett, M. (2007). Rhythm and beat perception in motor areas of the brain. Journal of Cognitive Neuroscience *19*, 893–906.

Grahn, J.A., McAuley, J.D. (2009). Neural bases of individual differences in beat perception. NeuroImage *47*, 1894–1903.

Grahn, J.A., Rowe, J.B. (2013). Finding and feeling the musical beat: striatal dissociations between detection and prediction of regularity. Cerebral Cortex *23*, 913–921.

Grube, M., Griffiths, T.D. (2009). Metricality-enhanced temporal encoding and the subjective perception of rhythmic sequences. Cortex *45*, 72–79.

Hannon, E. E., Trehub, S. E. (2005). Tuning in to musical rhythms: infants learn more readily than adults. Proceedings of the National Academy of Sciences *102*, 12639-12643.

Hoeschele, M., Merchant, H., Kikuchi, Y., Hattori, Y., ten Cate, C. (2015). Searching for the origins of musicality across species. Philosophical Transactions of the Royal Society B: Biological Sciences *370*, 20140094.

Hulse, S.H., Humpal, J., Cynx, J. (1984). Discrimination and generalization of rhythmic and arrhythmic sound patterns by European starlings (*Sturnus vulgaris*). Music Perception *1*, 442–464.

Hulse, S. H., Page, S. C., & Braaten, R. F. (1990). An integrative approach to auditory perception by songbirds. In W. C. Stebbins, M. A. Berkley (Eds.), Wiley series in neuroscience, Vol. 2. Comparative perception, Vol. 2. Complex signals. Oxford, England: John Wiley & Sons. pp. 3-34.

Kuhl, P.K. (2003). Human speech and birdsong: communication and the social brain. Proceedings of the National Academy of Sciences *100*, 9645–9646.

Patel, A.D. (2006). Musical rhythm, linguistic rhythm, and human evolution. Music Perception *24*, 99–104.

Patel, A.D., Iversen, J.R., Chen, Y., Repp, B.H. (2005). The influence of metricality and modality on synchronization with a beat. Experimental Brain Research *163*, 226–238.

Povel, D.J., Essens, P. (1985). Perception of temporal patterns. Music Perception *2*, 411–440.

Povel, D.J., Okkerman, H. (1981). Accents in equitone sequences. Perception & Psychophysics *30*, 565–572.

Randel, D.M., Apel, W. (1986). The new Harvard dictionary of music. Cambridge, MA: Belknap Press of Harvard University Press.

Schachner, A. (2013). If horses entrain, don't entirely reject vocal learning: an experience-based vocal learning hypothesis. Empirical Musicology Review *7*, 157.

Shmulevich, I., Povel, D.J. (2000). Measures of temporal pattern complexity. Journal of New Music Research *29*, 61–69.

Shu-Jen, K., Chen, J.L., Zatorre, R.J., Penhune, V.B. (2013). Interacting cortical and basal ganglia networks underlying finding and tapping to the musical beat. Journal of Cognitive Neuroscience *25*, 401–420.

Su, Y. H., Pöppel, E. (2012). Body movement enhances the extraction of temporal structures in auditory sequences. Psychological Research *76*, 373–382.

ten Cate, C., Spierings, M., Hubert, J., Honing, H. (2016). Can birds perceive rhythmic patterns? A review and experiments on a songbird and a parrot species. Frontiers in Psychology *7*, 730.

Vuust, P., Witek, M.A.G. (2014). Rhythmic complexity and predictive coding: a novel approach to modeling rhythm and meter perception in music. Frontiers in Psychology *5*, 1111.

van der Aa, J., Honing, H., ten Cate, C. (2015). The perception of regularity in an isochronous stimulus in zebra finches (*Taeniopygia guttata*) and humans. Behavioural Processes *115*, 37–45.

van der Weij, B., Pearce, M.T., Honing, H. (2017). A probabilistic model of meter perception: simulating enculturation. Frontiers in Psychology *8*, 824.

Webb, D.M., Zhang, J. (2005). FoxP2 in song-learning birds and vocal-learning mammals. Journal of Heredity *96*, 212–216.

Weisman, R., Njegovan, M., Sturdy, C., Phillmore, L., Coyle, J., Mewhort, D. (1998). Frequency-range discriminations: special and general abilities in Zebra finches (*Taeniopygia guttatd*) and Humans (*Homo sapiens*). Journal of Comparative Psychology *112*, 244–258.

Wilbrecht, L., Fernando, N. (2003). Vocal learning in birds and humans. Mental Retardation and Developmental Disabilities Research Reviews *9*, 135–148.

Appendix

Tables

Table 1. Task instructions provided to human participants in the explicit instructions experiment, including both the verbal instructions that were read aloud by the experimenter from a script and the instructions that were displayed onscreen. Italic text differs between the experiments and mostly concerns explicit mention of the beat, the requirements of the task and the category rules.

Explicit Instructions

Verbal Script:

1. For this experiment you are going to be listening to sounds and sorting each sound that you hear into one of two categories. *You will need to pay attention to the "beat" in each sound. The beat is the regular pulse that you feel while listening, for example like what you would feel in a piece of upbeat music. Each beat event is always spaced an equal amount of time apart.*
2. *Each of the sounds that you hear will either produce a strong or weak sense of beat – it is your job to sort the strong beat sounds from the weak beat sounds.*
3. Before the experiment begins, you will hear examples of sounds with a strong and weak beat to familiarize you.
4. To play a sound, first you must press the space bar. After the sound ends, *you must decide if the sound had a strong beat or a weak beat. If the sound had a strong beat,* you must press 1 (the red circle) on the keyboard to sort the sound into category A. *If it had a weak beat,* you must press 9 (the blue circle) to sort the sound into category B.
5. The experiment is broken up into two parts, followed by another short task at the end. The whole thing should take approximately 1 hour, though 1.5 hours is allowed in case you require additional time.
6. If you need to take a break at some point please let me know. The trials are self-initiated, meaning you must first press the space bar to play a sound, so feel free to pause for a moment if you need to rest.
7. The volume has been pre-set on the laptop – however, you are free to adjust it to a comfortable setting using the buttons in the top left corner of the keyboard.
8. One last thing - this is VERY important - while completing this experiment please remain as still as possible.
9. Please read the instructions displayed on screen and let me know if you have any questions.

On-screen Instructions

1. Welcome to the experiment. You will be asked to sort sounds into two categories. Your answers will be given on the keyboard.
2. *This experiment will require you to pay attention to the beat in rhythmic sounds, in a similar way to how you might feel a beat in a piece of music. The beat is a repeated pulse that you feel while listening, always separated by an equal amount of time. Some of the sounds you will hear will make you feel a strong sense of beat, while in other sounds the beat will be weaker. Your job is to sort the sounds with a stronger beat into Category A and sort the sounds with a weaker beat into Category B. Each sound will be played twice, separated by a brief pause.*
3. Press spacebar to hear an example of a sound *with a strong beat*. The sound you just heard *has a strong beat and* belongs to Category A. Sort it into Category A by pressing 1 on the keyboard.
   Press spacebar to hear an example of a sound *with a weaker beat*. The sound you just heard *has a weaker beat and* belongs to Category B. Sort it into Category B by pressing 9 on the keyboard.
4. For each trial: First press spacebar to play a sound twice. After the sound ends, you must indicate which category the sound you heard belongs to. *If the sound had a strong beat, sort it into Category A by pressing 1. If the sound had a weak beat, sort it into Category B by pressing 9.*
5. In the bottom right corner of the screen a number indicates your score on the task. Your points balance begins at zero and increases every time you sort a sound into the correct category, but you will not earn points for incorrect responses. Your final score will be compared with others so try to earn as many points as you can.
6. While listening to the sounds, please remain as still as possible, and refrain from tapping a foot or finger, etc. You are now ready to begin the task.
7. [At the end of each training block] You are performing at the level of (Novice, Intermediate or Expert). Please read through the instructions again and pay close attention to the feedback you get after each response.
8. [At the start of the generalization task] For this task you will hear new sounds and most sort them into the same two categories as before. *If the sound has a strong beat, sort it into Category A by pressing 1. If the sound has a weaker beat, sort it into Category B by pressing 9.*
9. Your points balance from Task 1 will be reset. You will still earn points for correct responses. However, on some trials no feedback will be given, and your points balance will not change. You can score a maximum of 120 points – try to earn as many as you can!

Table 2. Task instructions provided to human participants in the implicit instructions experiment, including both the verbal instructions that were read aloud by the experimenter from a script and the instructions that were displayed onscreen. Italic text differs between the experiments and mostly concerns the requirements of the task and the category rules.

Implicit Instructions

Verbal Script

1. For this experiment you are going to be listening to sounds and sorting each sound that you hear into one of two categories. *All of the sounds in each category have something in common – it is your job to figure this out.*
2. Before the experiment begins, you will hear examples of sounds that belong in each category to familiarize you.
3. To play a sound, first you must press the space bar. After the sound has played, you can press 1 (the red circle) on the keyboard to sort the sound into Category A, or press 9 (the blue circle) to sort the sound into Category B.
4. The experiment is broken up into two parts, followed by another short task at the end. The whole thing should take approximately 1 hour, though 1.5 hours is allowed in case you need additional time.
5. If you need to take a break at some point please let me know. The trials are self-initiated, meaning you must first press the space bar to play a sound, so feel free to pause for a moment if you need to rest.
6. The volume has been pre-set on the laptop – however, you are free to adjust it to a comfortable setting using the buttons in the top left corner of the keyboard.
7. One last thing - this is VERY important - while completing this experiment please remain as still as possible.
8. Please read the instructions displayed on screen and let me know if you have any questions.

On-screen Instructions

1. Welcome to the experiment. You will be asked to sort sounds into two categories. Your answers will be given on the keyboard.
2. Press spacebar to hear a sample sound from Category A. The sound you just heard belongs to Category A. Sort it into Category A by pressing 1 on the keyboard.
   Press spacebar to hear a sample sound from Category B. The sound you just heard belongs to Category B. Sort it into Category B by pressing 9 on the keyboard.
3. For each trial: First press spacebar to play a sound – you will hear it twice. After the sound ends, you must indicate which category the sound you heard belongs to. To sort the sound into Category A press 1. To sort the sound into Category B press 9.
4. In the bottom right corner of the screen a number indicates your score on the task. Your points balance begins at zero and increases every time you sort a sound into the correct category, but you will not earn points for incorrect responses. Your final score will be compared with others so try to earn as many points as you can.
5. While listening to the sounds, please remain as still as possible, and refrain from tapping a foot or finger, etc. You are now ready to begin the task.
6. [At the end of each training block] You are performing at the level of (Novice, Intermediate or Expert). Please read through the instructions again and pay close attention to the feedback you get after each response.
7. [At the start of the generalization task] For this task you will hear new sounds and most sort them into the same two categories as before. Press 1 to sort the sound into Category A. Press 9 to sort the sound into Category B.
8. Your points balance from Task 1 will be reset. You will still earn points for correct responses. However, on some trials no feedback will be given, and your points balance will not change. You can score a maximum of 120 points – try to earn as many as you can!

Table 3. Counts of the number of occurrences of runs of intervals in the metric simple (MS) and metric complex (MC) categories. A run is defined as a series of three or more consecutive intervals contained within a stimulus pattern. Each possible run of three intervals (containing 1, 2, 3, 4) are listed (a total of 64 combinations) plus a single run of four intervals (1111) which was more common in the MS category. The majority of runs are approximately matched in frequency between the two categories; some runs are exactly matched. This balancing was to ensure that no other rule could be used to correctly discriminate between MS and MC.

Run	Count in MS	Count in MC	Run	Count in MS	Count in MC	Run	Count in MS	Count in MC	Run	Count in MS	Count in MC
1111	5	1	211	6	3	311	2	4	411	4	5
111	6	6	212	0	3	312	3	2	412	0	1
112	8	3	213	1	1	313	1	0	413	2	1
113	2	2	214	0	0	314	4	2	414	0	0
114	4	4	221	6	4	321	0	1	421	0	0
121	0	3	222	2	1	322	1	1	422	4	1
122	5	5	223	1	0	323	0	0	423	0	1
123	3	2	224	3	3	324	0	1	424	0	0
124	0	1	231	4	2	331	2	1	431	1	0
131	2	3	232	0	3	332	0	0	432	0	1
132	1	1	233	0	0	333	0	0	433	0	0
133	2	1	234	0	0	334	0	0	434	0	0
134	0	0	241	1	5	341	0	0	441	0	0
141	1	5	242	0	0	342	0	0	442	0	0
142	2	3	243	0	1	343	0	0	443	0	0
143	1	1	244	0	0	344	0	0	444	0	0
144	0	0									

Table 4. Counts of the number of stimuli within the metric simple (MS) and metric complex (MC) categories that begin and end with each of the possible intervals 1-4.

First interval in pattern	Count in MS	Count in MC	Last interval in pattern	Count in MS	Count in MC
1	4	11	1	7	10
2	6	5	2	8	7
3	6	5	3	1	3
4	6	1	4	6	2

Table 5. The debrief questionnaire administered to human participants following the generalization task. This table is condensed from the original two-page document, but questions are listed verbatim. Participants were free to leave any item blank. Questions 1-10 concern the experiment; questions 11-15 concern subject's musical background.

Question	Response (1-10 indicates rating)
1. How well did you understand the task?	1 = I understood very well what the task was. 10 = I did not understand the task.
2. How difficult did you find the task?	1 = The task was very easy. 10 = The task was very hard.
3. How strongly did you concentrate on the task?	1 = I was highly concentrated. 10 = I was not concentrated.
4. Did your concentration on the task changed throughout the experiment?	1 = My concentration did not change. 10 = My concentration strongly changed.
4.a If your concentration changed, in which direction did it change?	1 = My ability to concentrate improved 10 = My ability to concentrate declined
5. How motivated were you for the experiment?	1 = I was not motivated. 10 = I was highly motivated.
6. What proportion of the time were you uncertain of your response?	1 = I almost never guessed. 10 = I almost always guessed.
7. Did you find yourself moving along to the sounds? For example, nodding your head, tapping your finger or foot?	Yes/No
8. Did you use/develop any specific strategies during the experiment to solve the task?	Yes/No
9. If yes, please describe briefly.	
10. Do you have additional comments regarding the experiment?	
11. How would you describe your musical skills/experiences?	1 = not skilled/experienced. 10 = very skilled/experienced
12. Have you ever played a musical instrument?	Yes/No
(If yes) 12.a Which instrument(s)?	
12.b For how many years have you played?	
12.c What type of training did you receive? (ex. conservatory, private lessons, self-taught)	
12.d Are you currently practicing music?	Yes/No
12.e If yes, how many hours per week do you practice?	
13. How would you rate your own ability to sense the beat in a piece of music? For example, if you were asked to tap along in time to music, could you do so?	1 = very poor at picking up a beat. 10 = excellent at picking up a beat
14. How important is music to your identity?	1 = not important. 10 = very important
15. Do you listen to music regularly?	Yes/No
(If yes) 15.a How many hours per week do you listen to music?	
15.b Which genre(s) of music do you listen to?	

Table 6. Sessional data for each starling subject across the two operant experiments. For operant experiment 1, only sessions that took place after the finalized parameters for the testing procedure were in place. Calculations are based on the total number of trials in each session, including correction trials. Metrics exclude data from any sessions in which performance may have been negatively impacted by external factors, such as hardware malfunction, human error and interruptions due to environmental noise. Subjects marked with asterisks are those that underwent pilot previous to the first isochronous-triplet discrimination.

Operant Experiment 1

	Isochronous - Triplet				Metric Simple - Metric Complex			
Subject ID	Total count of trials	Number of sessions (to criterion)	Mean trials per session	St Dev trials per session	Total count of trials	Number of sessions (to criterion)	Mean trials per session	St Dev trials per session
Liszt	4,076	16	255	82	19,353	56	346	48
* Chopin	14,823	51	291	48	12,054	37	326	14
* Debussy	11,470	45	255	61	12,812	43	298	27
* Beethoven	12,896	49	263	44	11,610	39	298	41
Schubert	6,039	19	318	45	13,678	45	304	29
Vivaldi	4,612	21	220	60	15,287	51	300	34
Tchaikovsky	6,384	19	336	56	11,515	36	320	24
Bach	7,673	25	307	58	12,219	42	291	32

Operant Experiment 2

	Isochronous - Triplet Baseline Reacquisition				Test Probe Trials	
Subject ID	Total count of trials	Number of sessions (to criterion)	Mean trials per session	St Dev trials per session	Mean probe trials across probe sessions	StDev probe trials per session
Liszt	2,508	9	279	37	67	6
Chopin	9,007	32	281	21	59	5
Debussy	4,639	17	273	10	65	3
Beethoven	4,025	16	252	17	58	5
Schubert	2,134	8	267	13	65	4
Vivaldi	2,136	8	267	22	56	5
Tchaikovsky	5,758	23	250	26	62	6
Bach	6,133	22	279	20	65	5

Figures

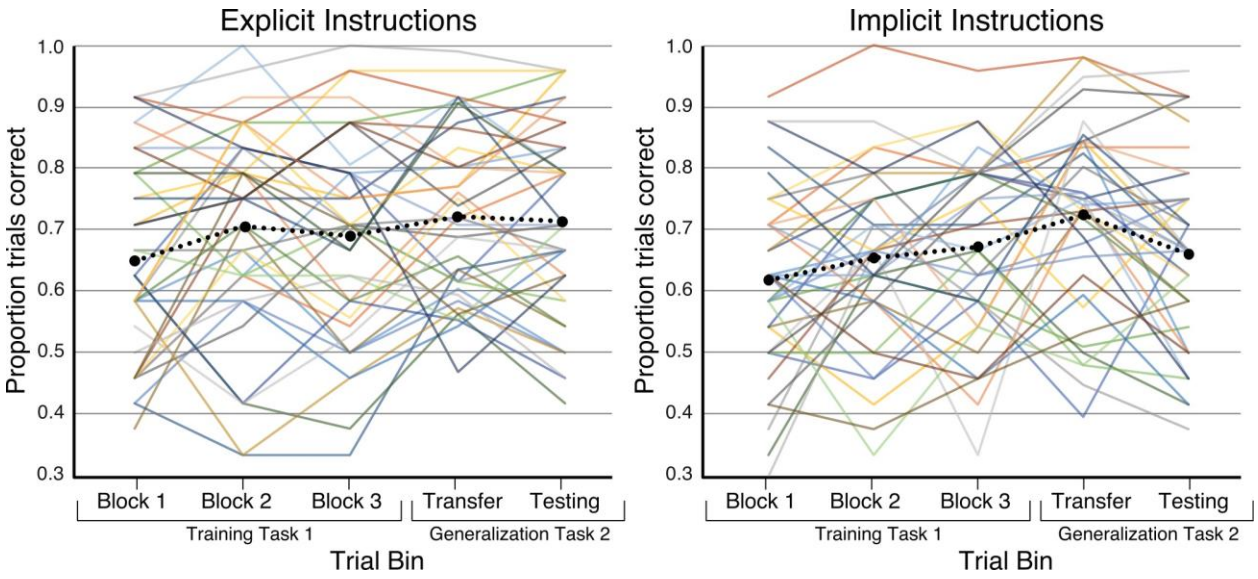

Figure 1. Accuracy scores on the training and generalization tasks for individual human participants in the explicit and implicit experiments. Each coloured line represents a single participant. The dotted black line shows mean accuracy within each trial bin averaging across subjects. A significant difference was found between performance in the explicit and implicit instructions experiments; scores and means from these experiments are depicted separately.

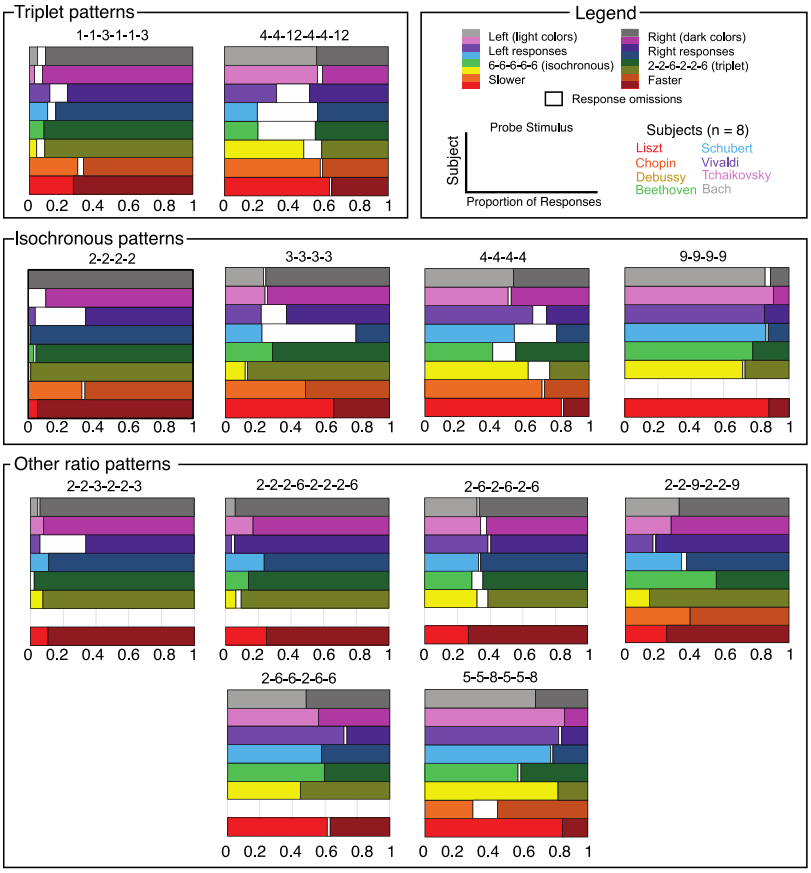

Figure 2. Responses of starling subjects to the probe stimuli in the second operant experiment. Patterns are plotted separately and are ordered within each category by increasing mean interval length. Each colour represents the responses of one subject. The lighter coloured (left) bars show the proportion of probe trials that the bird responded by pecking the left key, relating the probe stimulus to the baseline isochronous pattern. The darker coloured (right) bars show the proportion of probe trials that the bird responded by pecking the right key, relating the probe stimulus to the baseline triplet pattern. White gaps between the light and dark bars show the proportion of probe trials in which no response was recorded (omissions). Vertical alignment of the intersection between left and right bars indicates close agreement between subjects. Horizontal positioning of this intersection indicates the ratio between responses, which may be used to index how strongly the subjects related the probe stimuli to the baseline patterns.

Western

AUP Number: 2016-105 **PI Name:** Macdougallshackleton, Scott A
AUP Title: Sound perception of songbirds
Official Notification of ACC Approval: A MODIFICATION to Animal Use Protocol 2016-105 has been approved.

Please at this time review your AUP with your research team to ensure full understanding by everyone listed within this AUP.

As per your declaration within this approved AUP, you are obligated to ensure that:
1) Animals used in this research project will be cared for in alignment with:
   a) Western's Senate MAPPs 7.12, 7.10, and 7.15 http://www.uwo.ca/univse c/policies_procedures/research.html
   b) University Council on Animal Care Policies and related Animal Care Committee procedures
   c) http://uwo.ca/research/services/animalethics/animal_care_and_use_policies
2) As per UCAC's Animal Use Protocols Policy,
   a) this AUP accurately represents intended animal use;
   b) external approvals associated with this AUP, including permits and scientific/departmental peer approvals, are complete and accurate;
   c) any divergence from this AUP will not be undertaken until the related Protocol Modification is approved by the ACC; and
   d) AUP form submissions - Annual Protocol Renewals and Full AUP Renewals will be submitted and attended to within timeframes outlined by the ACC. http://uwo.ca/research/services/animalethics/animal_use_protocols.html
3) As per MAPP 7.10 all individuals listed within this AUP as having any hands-on animal contact will
   a) be made familiar with and have direct access to this AUP;
   b) complete all required CCAC mandatory training (training@uwo.ca);
   c) be overseen by me to ensure appropriate care and use of animals.
4) As per MAPP 7.15,
   a) Practice will align with approved AUP elements;
   b) Unrestricted access to all animal areas will be given to ACVS Veterinarians and ACC Leaders;
   c) UCAC policies and related ACC procedures will be followed, including but not limited to: i) Research Animal Procurement ii) Animal Care & Use Records iii) Sick Animal Response iv) Continuing Care Visits
5) As per institutional OH&S policies, all individuals listed within this AUP who will be using or potentially exposed to hazardous materials will have completed in advance the appropriate institutional OH&S training, facility-level training, and reviewed related (M)SDS Sheets, http://www.uwo.ca/hr/learning/required/index.html

Submitted by: Copeman, Laura
on behalf of the Animal Care Committee University Council on Animal Care

Curriculum Vitae

Brendon Samuels

EDUCATION

Master of Science Neuroscience
2016 – Expected 2018
The University of Western Ontario, London, ON.

Bachelor of Science with Honours Psychology: Brain & Cognition
2010 – 2014
University of Guelph, Guelph, ON.

SCHOLARSHIPS & AWARDS

Province of Ontario Graduate Scholarship (OGS), 2019.

Best Poster Award, Biology Graduate Research Forum, The University of Western Ontario, 2017.

Dean's List Honours, University of Guelph, 2012-2014.

RESEARCH EXPERIENCE

Masters Research The University of Western Ontario, London, ON, 2016 – 2018.
- Designed, programmed and executed behavioural experiments with human participants at the Brain and Mind Institute
- Operant testing, care of wild-caught birds at the Advanced Facility for Avian Research
- Supervised by Dr. Jessica Grahn and Dr. Scott MacDougall-Shackleton

Research Assistant York University, Toronto, ON, 2014.
- Sensorimotor control lab under the supervision of Dr. Denise Henriques
- Executed behavioural experiment using InMotion2 two-joint robot manipulandum

Undergraduate Honors Research University of Guelph, Guelph, ON, 2013-2014.
- Supervised by Dr. Naseem Al-Aidroos in the Visual Cognitive Neuroscience Lab
- Collaboration with two graduate students on an experiment testing implicit learning of visual statistical regularities using EyeLink 2 eye-tracking equipment

Undergraduate Research, University of Guelph, Department of Psychology, 2013.
- Two group research projects with focus on quantitative results reporting
    - Designed and executed an online survey examining relationships between lifestyle factors and symptoms of Seasonal Affective Disorder (SAD)
    - Behavioural study testing differences between sensory modalities for encoding semantic information into short-term memory

CONFERENCE ACTIVITIES

Poster Presentations

B. Samuels, J. Grahn, S. MacDougall-Shackleton, M. Henry. *Discriminating between strong and weaker beats in temporal patterns.* Southern Ontario Neuroscience Association, Regional Conference, February 2018. Niagara Falls, ON.

B. Samuels, J. Grahn, S. MacDougall-Shackleton, M. Henry. *Discriminating between strong and weaker beats in temporal patterns.* Lake Ontario Visionary Establishment Conference, Provincial Conference, February 2018. Niagara Falls, ON.

B. Samuels, J. Grahn, S. MacDougall-Shackleton, M. Henry. *The Birds and the Beats: Can songbirds perceive regularity in rhythmic auditory sequences?* Biology Graduate Research Forum, Western Institutional Conference, October 2017. London, ON.

B. Samuels, J. Grahn, S. MacDougall- Shackleton, M. Henry. *Can songbirds perceive regularity in rhythmic auditory sequences?* Southern Ontario Neuroscience Association, Regional Conference, May 2017. Brock University, St Catherines, ON.

B. Samuels, J. Grahn, S. MacDougall-Shackleton, M. Henry. *The Birds and the Beats: Perception of a Beat in an Avian Model.* Western Research Forum, Institutional Conference, March 2017. London, ON.

A. Daoust, **B. Samuels**, J. McAnnich, K. McAuley, M. Painter, E. Xu. *Effects of lexical encoding modalities on working memory.* Psychology Department Undergraduate Research Symposium, December 2013. Guelph University, Guelph, ON.

Oral Presentations

B. Samuels, S. MacDougall-Shackleton, J. Grahn. *Do Birds That Tweet Also Feel Beat? Perception of Temporal Patterns in the Common Starling.* International Ornithological Congress (IOC), International Meeting, August 2018. Vancouver, BC.

B. Samuels, S. MacDougall-Shackleton, J. Grahn. *Do Birds That Tweet Also Feel Beat? Perception of Temporal Patterns in a Songbird.* Animal Behaviour Society Meeting (ABS) International Meeting, August 2018. Milwaukee, Wisconsin, USA.

B. Samuels, S. MacDougall-Shackleton, J. Grahn. *Perception of Temporal Accents in Acoustic Patterns: Do Songbirds Feel the Beat?* Ontario Ecology, Ethology & Evolution Colloquium, Provincial Meeting, May 2018. London, ON.

B. Samuels, J. Grahn, S. MacDougall-Shackleton, M. Henry. *Can songbirds discriminate between sounds that contain strong and weak beats?* Neural Entrainment Rhythm Dynamics, June 2017. Boston, MA, USA.

B. Samuels, J. Grahn, S. MacDougall-Shackleton, M. Henry. *Detection of acoustic regularity in the absence of motor synchronization: Beat perception in a songbird.* Symposium on Timing And Rhythm, April 2017. Hamilton, ON.

Other Conferences Attended

Animal Behavior Society (ABS) Meeting. June 2017, Toronto, Ontario.

Lake Ontario Visionary Establishment Conference. February 2017, Niagara Falls, Ontario.

ACADEMIC ACTIVITIES

Teaching Assistantships

PSYC3130 Psychology of Thinking, The University of Western Ontario, Winter 2018.

PSYC1000 Introduction to Psychology, The University of Western Ontario, Fall 2017.

PSYC1000 Introduction to Psychology, The University of Western Ontario, Winter 2017.

PSYC1000 Introduction to Psychology, The University of Western Ontario, Fall 2016.

Outreach Initiatives

Gradcast Radio, The University of Western Ontario, October 2017.
- Interviewed about my ongoing Masters thesis research

Retiring with Strong Minds, The University of Western Ontario, June & September 2017.
- Presented my research to residents of two retirement communities

London Brain Bee, The University of Western Ontario, April 2017 & 2018.
- Demonstrations for high school students on research in neuroscience
- Organizing committee, created promotional materials, event photographer

TD Discovery Day in Health Sciences, The University of Western Ontario, May 2017.
- Offered research equipment demonstration for visiting high school students

SHAD Tour of Advanced Facility for Avian Research, July 2017.
- Offered demonstration of operant testing apparatus

Committee Contributions

Ontario Ecology, Ethology & Evolution Conference, Spring 2018.
- Conference organizing committee, production of art materials

Society of Neuroscience Graduate Students, 2017-2018.
- Founding member of executive committee
- Acting art director; web management, promotion and event planning

Graduate Student Teaching Award Selection Committee, Spring 2017.

Educational Activities

Summer School: Center for Vision Research, York University, Summer 2014.
- Seminars and demonstrations conducted by health, psychology and engineering research faculty; discussion of ongoing research projects

Neuroscience & Applied Cognitive Science Seminars, University of Guelph, 2013-2014.
- Biweekly seminars offered by psychology faculty & visiting researchers