ABSTRACT

Title of Document: CONTROL OF VOCAL PRODUCTION IN BUDGERIGARS (*MELOPSITTACUS UNDULATUS*)

Michael S. Osmanski, Ph.D., 2008

Directed By: Professor Robert J. Dooling, Department of Psychology

Budgerigars engage in dynamic vocal interactions with conspecifics, learn their vocalizations in a rich social environment, and rely to some extent on auditory feedback to acquire and maintain normal vocal output. However, little is known about the exact role of sensory input and sensory feedback in the control of vocal production in these birds. For example, we know that these birds learn best in a social environment that contains both auditory and visual information, yet we know very little about how this information guides and influences vocal production. Although we suspect that budgerigars rely on auditory feedback for the learning and maintenance of vocal behavior, we do not know whether there are refined, compensatory feedback mechanisms similar to that of humans. Finally, we do not know whether, or to what extent, calls can be modified in structure during learning. This dissertation describes a series of experiments that use more highly controlled and regimented conditions than previous studies with songbirds to investigate the control of vocal production in budgerigars and to provide a more detailed description of some of the mechanisms underlying vocal learning in budgerigars.

CONTROL OF VOCAL PRODUCTION IN BUDGERIGARS (*MELOPSITTACUS UNDULATUS*)

By

Michael S. Osmanski

Dissertation submitted to the Faculty of the Graduate School of the
University of Maryland, College Park, in partial fulfillment
of the requirements for the degree of
Doctor of Philosophy
2008

Advisory Committee:
Professor Robert J. Dooling, Chair
Professor Catherine E. Carr
Professor Cynthia F. Moss
Associate Professor Rochelle S. Newman
Professor Xiaoqin Wang

Preface

This dissertation has taken the form of individual papers which necessarily results in some redundancy in literature review and in details of methods and procedures. The following provides a succinct overview of the rationale and experimental questions addressed in this dissertation which you might find useful as a guide to focus on the critical aspects of the dissertation.

The most common vocalization in budgerigars is a short (~150 msec), high intensity (>~90 dB), frequency-modulated, tonal sound named the "contact call" - after its presumed function of keeping birds in contact with one another. Typically each bird produces one to several different (sonographically distinct) contact calls with the main or predominant contact call produced 80-90% of the time. Deafened birds produce aberrant contact calls. Budgerigars housed together in small groups often come to share (with a high degree of precision) the same contact call within several weeks. Budgerigars who hear, but don't see, other budgerigars typically do not share calls. Both males and females produce and learn contact calls throughout life. Many ethological and behavioral studies have shown that an isolated or individually housed budgerigar produces contact calls in response to seeing another budgerigar or hearing the vocalizations, especially contact calls, of another budgerigar. Birds produce contact calls almost exclusively within a loud flock environment containing many budgerigars vocalizing simultaneously. Budgerigars can also be trained to produce contact calls under operant control.

The above summarizes a huge amount of literature on vocal learning and vocal production in budgerigars. Operantly controlled vocal production is particularly relevant because it opens the door to new avenues of investigation into call learning and production. For example, we can ask whether calls are produced ballistically rather than under immediate feedback control. Under more rigorous experimental conditions of operant control, this dissertation examines some of the behavioral variables that control vocal modification and production in budgerigars. All but the initial experiment involves training birds to produce contact calls through operant conditioning and then manipulating either stimulus cues to vocal production, or auditory feedback conditions during vocal production, or reinforcement contingencies controlling vocal production. The main experiments are summarized below:

Experiment 1 conducted a fine grain analysis of calling behavior in pairs of birds who were not in visual contact. The point was to see which features of one bird's calling behavior were influenced by the other bird using only acoustic information. Neither the type of contact call nor the spectrotemporal form of the contact calls in one bird were influenced by the calling behavior of the other bird. This is consistent with the observation that birds do not learn calls from one another when they are not in visual/social contact.

Experiment 2 examined the relative salience of visual versus acoustic stimuli in cuing the production of different contact calls in budgerigars in an operant situation. Birds readily learned to associate production of two different contact calls to qualitatively

distinct visual cues and to spatially distinct visual or acoustic cues. However, they did not readily associate production of two different contact calls to qualitatively distinct acoustic cues. This is supportive of the results of Experiment 1 in a free calling situation and the hypothesis that birds don't learn from acoustic information alone.

Experiment 3 examined the effect of background noise on the intensity of vocal production (Lombard effect) in birds wearing earphones. This experiment confirmed the Lombard effect, extended it to a broader range of noise levels, and showed that increases in vocal level were accompanied by increases in pitch and duration. These results parallel those typically found in humans.

Experiment 4 tested whether altering the feedback level of self-produced vocalizations affected vocal production. Birds wearing earphones showed a robust Fletcher effect (a decrease in vocal amplitude in response to an increase in perceived vocal loudness). Call production amplitude decreased as feedback intensity increased and this effect was accompanied by decreases in call pitch and duration. These changes are consistent with those of Experiment 3 and parallel the results of similar experiments in humans. Interestingly, amplitude adjustments to increases in perceived loudness did not occur during vocal production but occurred on the subsequent vocalization.

Experiment 5 examined whether delayed auditory feedback (DAF) of the bird's own voice affected its vocal production. Results show that budgerigars respond by producing incomplete and/or distorted calls throughout a test session. The most effective delay was 25 ms, with longer and shorter delays producing fewer errors. Paralleling Experiment 4, DAF did not affect ongoing vocal production but did affect subsequent vocalizations. Taken together, results of Experiments 4 & 5 argue for a more ballistic mechanism in production of contact calls rather than one relying on the online monitoring of vocal production.

Experiment 6 examined the extent to which differential reinforcement of pitch changes resulted in the production of pitch-altered calls. Results show that birds can readily change the average pitch of their calls by changing smaller portions of the call (resulting in a ‘new’ call) but they cannot change the pitch of the entire call while maintaining its spectrotemporal pattern. These results highlight limitations of vocal plasticity in budgerigars.

Taken together, these experiments provide insights into mechanisms of budgerigar vocal learning and production and support the hypothesis that learning in these birds depends on social and/or visual stimuli. Calls may use an underlying auditory-vocal feedback mechanism that operates across calls rather than online within a call and that functions with significant limits, such as learning through piecemeal changes rather than global, wholesale changes. These results set the stage for future investigations of the learning and feedback systems of this species and exploration of further parallels to human behavior.

Dedication

To the countless family, friends, and colleagues that have helped me as I walked this long road. Without each of you, I would not have seen this dissertation completed. Thank you.

Acknowledgments

I would first like to thank my advisor, Bob Dooling, for his advice, guidance, and mentorship throughout my graduate career. I would also like to thank my entire dissertation committee - Catherine Carr, Cindy Moss, Rochelle Newman, Xiaoqin Wang - for all of their help and comments.

The friends and colleagues that I have gained during these years have undoubtedly been one of the greatest gifts I have received. In addition to my committee members, I thank Sandra Blumenrath, Stacey Brown, Kristina DeAngelo, Micheal Dent, Amanda Lauer, Bernie Lohr, Peter Marvit, Ed Smith, Manjit Sahota, Jeff Triblehorn, Vicky Tu, Beth Vernaleo, Tim Wright, and Dave Yager for their generous insights, encouragement, and friendship over the years. Beth Brittan-Powell deserves special mention here – she has become one of my closest and most trusted allies and her support has been invaluable. I would not be here today without her knowledge, patience, and help. I also received assistance running experiments and collecting data from Kevin Budman, Christine Chapa, and especially Leah Dickstein – and I thank each of them.

Finally, I want to give a special acknowledgment to Elizabeth Osmanski. She has been a support to me throughout these several years – mentally, emotionally, and physically – and I can honestly say that none of this would have been possible were it not for her compassion, generosity, kindness, and love.

Table of Contents

List of Tables

Chapter 2

Chapter 4

Chapter 5

List of Figures

Chapter 2

Chapter 3

Chapter 4

Chapter 5

Chapter 1 – General Introduction

A. Vocal Learning

Vocal learning occurs when vocalizations are either modified in form or created anew as a result of social experience (Boughman and Moss, 2003; Farabaugh and Dooling, 1996; Janik and Slater, 1997, 2000). Only humans, oscine songbirds, and parrots show vocal learning, although there is some evidence for it in hummingbirds (Baptista and Schuchmann, 1990; Gahr, 2000), cetaceans (Richards *et al.*, 1984), and certain bats (Boughman, 1998; Jones and Ransome, 1993). All vocal learners live in complex, interactive social groups and depend on sensory feedback of self-produced vocalizations, especially auditory feedback, for normal vocal production.

The vast majority of animal species show no compelling evidence for vocal learning. Monkeys and cats show no obvious changes in vocal development or behavior when deafened (Romand and Ehret, 1984; Shipley *et al.*, 1988; Talmage-Riggs *et al.*, 1972). However, many species that do not learn to produce novel signals, the hallmark of vocal learning, nonetheless show contextual learning abilities. Contextual learning is the ability to associate existing vocalizations with new contexts or stimuli and has been shown in primates (Miller and Wang, 2006; Seyfarth and Cheney, 1986; Seyfarth *et al.*, 1980; Zuberbühler, 2000), ground squirrels (Owings and Leger, 1980; Owings and Virgina, 1978), domestic fowl (Gyger *et al.*, 1987), and male frogs of the group *Rana* (Gerhardt, 1994).

B. Avian Vocal Learning

Almost half of the more than 9,000 species of birds show vocal learning to some degree. More than half do not. Domestic fowl, ring doves, and eastern phoebes, for instance, show no change in vocal structure after deafening (Konishi, 1963; Kroodsma and Konishi, 1991; Nottebohm and Nottebohm, 1971). In contrast, all oscine songbirds and parrots rely on sensory feedback to develop and maintain normal vocalizations throughout life. Both groups have complex vocal repertoires that are learned in social contexts and depend on a normally-functioning auditory system (Brittan-Powell *et al.*, 1997; Cunningham and Baker, 1983; Doupe and Kuhl, 1999; Farabaugh and Dooling, 1996; Heaton *et al.*, 1999; Konishi, 2004; Marler, 1970; Thorpe, 1958; Williams, 2004)

1. *Songbirds*

Vocal learning in songbirds consists of two basic steps. First, young birds are exposed to and memorize the songs produced by adult conspecifics – usually the father or close neighbors. Second, the birds slowly modify a relatively unstructured vocalization until it approximates the memorized song (Konishi, 1965b; Marler, 1970). Research on this subject dates back to the classic song learning studies by Marler and colleagues in which birds learned by listening to tutor songs played through loudspeakers (Konishi, 1965b; Marler, 1970, 1981; Marler and Peters, 1977). Many species deviate somewhat from this basic learning trajectory. For example, the two learning stages may be separate or may overlap. The entire learning process may be complete by fledging or may occur across multiple breeding seasons. Song may remain fixed after the initial acquisition (as in zebra finches) or new songs and/or song elements may be learned each new year (as in canaries) or even throughout life (as in starlings - Hausberger, 1997) (for a brief review, see Williams, 2004).

2. *Songs vs. Calls*

Research on oscines has focused on song primarily because it is learned, stereotyped, and extremely amenable to both behavioral and neurophysiological study. However, songs represent only a small fraction of a species' vocal repertoire. Most birds produce a variety of different calls, which have been largely ignored in this field of study but, ironically, are perhaps better suited for such investigations (see Marler, 2004). Bird calls are often simple in structure, making them easier to analyze, manipulate and synthesize than song (Marler, 2004; Vicario, 2004). Calls are more diverse, are produced in a greater number of contexts and across a larger suite of behaviors, and serve a more diverse set of functions compared to song (Marler, 2004). Because calls can be elicited by a more varied set of environmental stimuli than song, they are also more appropriate for studies of stimulus-response associations in vocal production. More importantly, calls, like songs, are learned in many species (Hughes *et al.*, 1998; Mammen and Nowicki, 1981; Marler, 2004; Vicario, 2004; Zann, 1990, 1996).

3. *Budgerigars*

Parrots are the second largest order of birds that show vocal learning. Unlike songbirds, research on vocal learning in parrots has focused mostly on call learning. Parrot vocal learning evolved independently of the songbird order and, like song, is highly complex and remarkably amenable to investigations into its production and use as a communication signal (Brittan-Powell *et al.*, 1997; Farabaugh and Dooling, 1996; Kroodsma and Miller, 1982; Nottebohm, 1972; Striedter, 1994). Both laboratory and field studies describe inter- and intra-specific vocal imitation, individually-unique vocal repertoires, the perception and production of learned vocalizations, geographic variation, regional dialects, and pair duetting in these birds (Wanker and Fischer, 2001; Wright, 1996; Wright and Dorin, 2001; Wright and Wilkinson, 2000). Studies of parrot vocal behavior provide an opportunity to study the production, perception, and learning of vocalizations in a non-songbird species, and comparative studies between parrots, songbirds, and humans add to our knowledge of the structure, function, and evolution of learned vocal communication systems.

Budgerigars are the best-studied parrots in terms of their auditory capabilities, vocal behavior, and vocal learning (see review in Farabaugh and Dooling, 1996) and vocal learning in these birds may be more analogous to human speech and language than songbirds in several ways. Vocal learning in songbirds is usually restricted to males, to particular developmental stages and/or seasons, and to very discreet social environments. Budgerigar vocal learning, however, occurs over the course of days to weeks, has been reported in both males and females, and is independent of age and season (e.g., Brittan-Powell *et al.*, 1997; Brockway, 1964a; 1964b; 1969; Farabaugh and Dooling, 1996; Farabaugh *et al.*, 1992; Farabaugh *et al.*, 1994; Hile *et al.*, 2000; Hile and Striedter, 2000; Striedter *et al.*, 2003; Wyndham, 1980).

C. External Control of Vocal Production

1. *Social Experience in Vocal Learning*

Both laboratory and field studies show that vocal learning and vocal production in songbirds are controlled by a suite of external stimuli, especially in the auditory and visual domains, in a rich social milieu (Baptista and Gaunt, 1997; Brenowitz and Beecher, 2005; Nelson, 1997; Williams, 2004). For example, song sparrows sing particular song-types in response to the song-types produced by territorial neighbors (Beecher *et al.*, 1996) and male singing behavior is elicited by the sight of females in many songbird species (Takahasi *et al.*, 2005; West and King, 1988; Zann, 1996). Many species require social interaction with live conspecifics in order to learn song, while others will learn from a model bird that they can interact with (Baptista and Petrinovich, 1984; Tchernichovski *et al.*, 2001; Zann, 1996). Social experience drives learning so strongly in some species that they will preferentially learn the song of heterospecifics that they can interact with over conspecific song played through a loudspeaker (Baptista and Petrinovich, 1984; Payne, 1981).

Social experience also plays a critical role in parrot vocal learning. Food and social rewards can produce elaborate vocal modifications in both African grey parrots and budgerigars (Banta Lavenex, 2000; Pepperberg, 1993). In budgerigars, learning occurs during changes in social settings, especially during the addition and removal of flockmates (Brown *et al.*, 1988; Farabaugh *et al.*, 1994; Hile *et al.*, 2000; Hile and Striedter, 2000; Striedter *et al.*, 2003). These birds learn better from cagemates that they can interact with (even isolates and heterospecifics) instead of non-cagemates that they only have auditory experience with (Brittan-Powell *et al.*, 1997; Farabaugh *et al.*, 1994).

2. *Vocal Responses to Environmental Stimuli*

The relative influence of different environmental stimuli on the control of vocalizations is near impossible to tease apart in a natural context. Vocal learning and vocal production requires an interactive relationship between an animal's vocal behavior and environmental stimuli, but very little attention is paid to the specific pairings between these stimuli and the vocal responses they elicit (Nelson, 1997). The precise sensory input required for learning and how those stimuli trigger associations with vocal behavior is known in only a few cases. For example, the rapid wing movements and postural displays of female cowbirds signal a preference for specific song types, and males modify their vocal output in response to these visual signals in order to increase their attractiveness to females (West and King, 1988).

All birds must process environmental stimuli across a number of sensory modalities when selecting appropriate vocal responses during learning. In budgerigars, we know both auditory and visual information is important in this process (Farabaugh *et al.*, 1994). Unfortunately, the precise role of these sensory modalities and the specific stimulus-response pairings between environmental stimuli and vocal production remain largely unknown. For example, we know that budgerigars attend to the acoustic features of conspecific vocalizations (Brown *et al.*, 1988) and that conspecific facial features are salient to these birds (Brown and Dooling, 1992; 1993), but we do not know how, or to what extent, these features become associated with vocal behavior or drive vocal learning in social settings.

D. Internal Control of Vocal Production

1. *Neural Specializations for Vocal Learning*

Both songbirds and parrots have specialized neural structures that control vocal learning and vocal production, and these structures show similarities to brain areas underlying human speech learning (Jarvis, 2004, 2006). Songbirds have a group of specialized forebrain nuclei, collectively known as the song system, that comprise two basic pathways, each described from tract tracing, neurophysiological, and immediate-early gene-expression studies (Clayton, 2004; Doupe and Kuhl, 1999; Mello, 2002; Nottebohm, 1999). The first is a *posterior pathway* representing descending flow of efferent information. Lesions to this pathway result in an inability to produce song, although a bird may still adopt normal singing postures and beak movements (Nottebohm *et al.*, 1976). The second pathway, the *anterior forebrain pathway (AFP)*, represents a loop through striatal, thalamic, and pallial structures. This pathway is implicated in vocal learning processes (Bottjer, 2004; Brainard, 2004; Nordeen and Nordeen, 2004). Lesions to nuclei in the *AFP* result in premature crystallization of song in juvenile, but not adult, zebra finches and an inability to learn new springtime syllables in canaries. Thus, *AFP* nuclei are involved in the initial acquisition and later modification of learned song while the *posterior pathway* is responsible for song production.

Parrots have forebrain vocal control nuclei that are analogous to those described for songbirds (Brauth *et al.*, 1994; Durand *et al.*, 1997; Jarvis, 2004, 2006; Jarvis and Mello, 2000; Striedter, 1994). Like the oscine song system, there are two known neural pathways: A *posterior pathway* responsible for descending output from the system and an *anterior pathway* through pallial, striatal, and thalamic structures. Neurophysiological, lesion, and immediate-early gene expression studies in budgerigars show that, as in songbirds, the anterior nuclei provide the substrate for vocal learning (Banta Lavenex, 2000; Brauth *et al.*, 2002; Heaton and Brauth, 2000; Plummer and Striedter, 2002). Lesions to this group of nuclei result in lowered fundamental frequency, loss of learned spectrotemporal call structure, and loss of learned amplitude-modulation patterns (Banta Lavenex, 2000; Heaton and Brauth, 2000). Striatal nuclei are necessary for the learning of new calls and the maintenance of stereotypy in existing calls (Plummer and Striedter, 2002).

The budgerigar *anterior pathway* contains several additional connections and structures not present in the songbird system. This complex circuitry may underlie much of the lifelong vocal plasticity in parrots (see Durand *et al.*, 1997). Interestingly, human speech processing is also known to depend on structures that form cortical-striatal-thalamic loops, also analogous to the avian *AFP*, that are implicated in the learning and maintenance of vocal motor sequences (Jarvis, 2004, 2006; Jürgens, 1992, 1995; 2002; Lieberman, 2002).

2. Auditory Feedback

Vocal learners monitor and control their on-going vocal output using auditory feedback (AF). Deviations between the actual feedback and expected feedback result in an error signal which is then used to adjust subsequent vocal output. Thus, AF enables specific, dynamic, and compensatory responses to small fluctuations in the vocal signal and represents the best-documented example of sensory-motor interaction in any vocal behavior.

Humans

Human speech production is dependent on AF. For example, humans increase voice intensity in response to an increase in background noise level – a phenomenon called the Lombard effect (Lane and Tranel, 1971; Lombard, 1911; Ringel and Steer, 1963; Summers *et al.*, 1988). Speakers also decrease their voice intensity as perceived feedback loudness increases, a response known as the Fletcher effect (Lane and Tranel, 1971). These compensatory amplitude adjustments occur within 150-200 milliseconds of altered AF presentation (Bauer *et al.*, 2006; Heinks-Maldonado and Houde, 2005) and provide evidence that humans dynamically maintain a high signal-to-noise ratio between speech and ambient noise levels.

Temporal and spectral manipulations to speech feedback also perturb vocal output. Delaying the feedback signal (i.e., delayed auditory feedback [DAF]) by 200 milliseconds creates a number of speech dysfluencies, including a slower speech rate, higher fundamental frequency, longer syllable durations, and a range of production errors (Howell and Archer, 1984; Lee, 1950; Yates, 1963). These errors include stuttering and short consonant-like bursts of sound. Some subjects report a complete inability to continue speaking. Similarly, shifting AF upward or downward in pitch (i.e., pitch-shifted feedback) results in speakers reciprocally raising or lowering their voice pitch (Burnett *et al.*, 1998; Elman, 1981). This response occurs within approximately 150 milliseconds of shift onset.

Songbirds

We know birds depend on AF for the learning and maintenance of song (see Brainard and Doupe, 2000). Crystallized zebra finch song, once thought to be impervious to alteration (Price, 1979), degrades after 6-8 weeks following bilateral cochlear removal (Lombardino and Nottebohm, 2000; Nordeen and Nordeen, 1992). Deafened birds show a loss of stereotypy in syllable structure, deletion and repetition (e.g., 'stuttering') of syllables, and incorporation of novel syllables into their song. Leonardo and Konishi (1999) played temporally-misaligned song to singing zebra finches and found similar distortions and perturbations that increased in severity over several weeks. A series of related experiments in Bengalese finches showed a loss of syllable ordering within a week and a loss of syllable structure within 2 weeks following bilateral cochlear removal (reviewed in Okanoya and Yamaguchi, 1997; Woolley, 2004; Woolley and Rubel, 1997).

Real-time processing of auditory feedback during ongoing vocal production has recently been demonstrated in songbirds. Error rates increase immediately in male zebra finches in response to DAF, with the greatest number of errors occurring at a delay of 100 milliseconds (Cynx and Von Rad, 2001); errors are similar to those described in (Nordeen and Nordeen, 1992). Similar effects have more recently been reported in Bengalese finches (Sakata and Brainard, 2006). Disruptions in syllable structure and sequencing affect Bengalese finches exposed to temporally-misaligned auditory feedback within 60-90 milliseconds of feedback onset, with the most effective delay around 40-65 milliseconds.

Budgerigars

The role of AF in budgerigar vocal production is less understood compared to humans and songbirds. Budgerigars show a robust Lombard effect, raising the intensity of their vocalizations in response to an increase in ambient noise level in the free-field (Manabe *et al.*, 1998). They also show a profound degradation in vocal production and in their ability to maintain vocal precision when deafened as nestlings and adults (Dooling *et al.*, 1997; Heaton and Brauth, 1999; Heaton *et al.*, 1999). Similar vocal degradation and loss of stereotypy occurs following lesions to nucleus basalis, which is believed to be the main source of ascending auditory input to telencephalic vocal centers (Hall *et al.*, 1994).

3. *Models of the Auditory Feedback Effect*

Several authors have proposed models of the AF mechanisms underlying vocal learning in humans and songbirds. Most of these describe an open-loop feedback system in which AF is used to guide subsequent vocal-motor gestures in real-time (e.g., Brainard and Doupe, 2000; Burnett *et al.*, 1998; Guenther, 2001; Lee, 1950; Margoliash, 2002; Mooney, 2004; Neilson and Neilson, 1991; Sakata and Brainard, 2006; Troyer and Doupe, 2000a; 2000b). Both Guenther's (2001) DIVA model of human speech and Troyer and Doupe's (2000a; 2000b) model of birdsong, for instance, posit an internal reference sent from premotor areas associated with vocal production to auditory areas. This reference is then compared with incoming auditory information. Differences between the expected and obtained vocalizations constitute an error signal which is then used to correct aberrant vocalizations.

There are two principle problems inherent in these real-time models of auditory feedback (Borden, 1979; Margoliash, 2002). First, there is a general failure to account for why the speech of hearing-impaired humans and deafened songbirds does not degrade immediately. The loss of on-line feedback in these situations presumably would disrupt ongoing vocal behavior rather abruptly. Second, these models do not account for the fact that, because of the rapid production rates of birdsong and human speech, the minimum time required for auditory feedback of a vocal gesture (i.e., a syllable) to reach comparison centers in the brain is longer than the mean duration of that vocal gesture. In other words, the next syllable is already being produced by the time the auditory feedback of the previous syllable reaches the comparator. This means that auditory feedback cannot be used as a compensatory mechanism within a short vocal gesture.

Various authors propose alternative solutions to the inherent problems of online auditory feedback models. Most of these solutions simply involve a feed-forward mechanism in which a stored version of the outgoing motor program is used for future comparisons with auditory feedback, enabling vocal production to operate independently of real-time feedback (see Konishi, 2004; Lashley, 1967; Margoliash, 2002; Sakata and Brainard, 2006; Troyer and Doupe, 2000b). For songbirds, some researchers have suggested that auditory feedback of vocal gestures is used completely offline and that learning occurs through a process analogous to proposed mechanisms of REM sleep-associated memory consolidation in humans (Dave and Margoliash, 2000; Margoliash, 2002). One model of speech production by Howell and colleagues (Howell, 2002; Howell and Sackin, 2002) describes a combination online-offline feedback system in humans containing a central pattern generator (CPG) which supplies the millisecond-to-millisecond timing of speech output independently of real-time auditory feedback (which is why vocal behavior does not degrade immediately after deafening) along with feedback inputs to the CPG which allow for immediate, compensatory responses to deviant productions (which is why altered auditory feedback produces effects within milliseconds to seconds).

4. *Units of Production and Auditory Feedback Timing*

AF models depend on understanding how real-time processing of feedback controls vocal production and guides changes in the acoustic structure of vocalizations. Songbirds, for instance, learn through a process in which changes are made at the level of song elements and not at the level of whole songs. Zebra finches do not learn song through wholesale imitation of the tutor but, instead, learn individual syllables – each at potentially different rates – in a process of gradual change marked by abrupt transitions (e.g., period doubling) (Deregnaucourt *et al.*, 2004; Tchernichovski *et al.*, 2001). Other data show that syllables are the minimal units of production in birdsong. Brief flashes of light interrupt song production between, but not within, syllables (Cynx, 1990; Riebel and Todt, 1997), and studies of respiratory patterns during singing behavior show that syllables are generated by a single expiration (Franz and Goller, 2002). These results suggest that each syllable represents a single vocal motor gesture and are probably produced in a ballistic fashion.

The AF response to manipulations in amplitude and pitch in humans occur 150-200 milliseconds after stimulus onset, and a temporal misalignment of 200 milliseconds between AF and ongoing speech severely disrupts vocal output. These timescales are on the order of a normal speech syllable. The onset delay for DAF effects in songbirds is also approximately the length of a syllable (Cynx and Von Rad, 2001; Sakata and Brainard, 2006). Thus, humans and birds likely do not make compensatory changes to ongoing syllables based on AF, but instead adjust subsequent syllables produced after feedback onset.

It is not currently known whether budgerigars produce contact calls through a ballistic mechanism or whether calls can be adjusted online. There is evidence that calls are comprised of a series of short, elementary segments – like zebra finch songs and human speech. For example, different contact calls may share some or all of the same acoustic elements and call learning is achieved through a process of convergence whereby calls produced by different birds come to resemble one another through modification of call segments (Farabaugh *et al.*, 1994; Hile *et al.*, 2000; Hile and Striedter, 2000). However, the minimal units of production for contact calls have yet to be determined and we don't know whether birds learn calls through piecemeal changes to individual call segments or by making more global changes across the entire call. Thus, it is possible that calls are produced in a ballistic manner analogous to the individual syllables that make up birdsong and speech.

No studies to date have looked at real-time processing of auditory feedback during ongoing vocal production in budgerigars to examine whether there is an online effect of feedback. Budgerigar contact calls have an average duration of approximately 150 milliseconds – roughly similar to the length of syllables in human speech (~200 ms- e.g., Greenberg, 1999) and zebra finch song (~100 ms- e.g., Glaze and Troyer, 2006). AF effects in budgerigars will likely operate at similar timescales as humans and songbirds. Thus, budgerigars may not show real-time changes in call production and this could be because either 1) the mean call duration is too short or 2) contact calls are not susceptible to online modification.

E. Summary

Our understanding of the behavioral mechanisms of avian vocal learning lacks the precision and detail of the human literature because of technical limitations inherent in animal work. Vocal learning in birds is typically studied by broadly manipulating the acoustic and/or social experience in these animals, including controlling or restricting access to live conspecifics (Baptista and Gaunt, 1997; Brittan-Powell *et al.*, 1997; Farabaugh *et al.*, 1994; Nelson, 1997), cochlear removal (Dooling *et al.*, 1987; Heaton and Brauth, 1999; Konishi, 1965a; 1965b) syringeal denervation (Heaton *et al.*, 1995), syringeal obstruction (Hough and Volman, 2002), and free-field playback of song during uncontrolled vocal behavior (Leonardo and Konishi, 1999). These manipulations are relatively coarse in nature and often confounded because they disrupt a broad suite of behaviors. What is needed is a more controlled approach toward examining the mechanisms underlying sensory associations and sensory feedback in vocal production.

This dissertation describes a series of experiments using highly refined and controlled conditions to examine the role of specific environmental stimuli and sensory feedback on vocal behavior in budgerigars. Determining the stimuli that drive vocal production in previous experiments would have been difficult because of the complexity of an animal's social milieu. Similarly, looking at the role of auditory feedback in vocal learning would normally have been severely limited by the lack of stimulus control common in previous experiments. However, I have succeeded in bringing vocal behavior in these birds under operant control using conditioning methods similar to those of Manabe and colleagues (2008; 1995; 1997). Such methods allowed me to control aspects of vocal behavior in these animals, including the number of vocalizations produced and/or heard, the timing of vocal production, the acoustic and visual stimuli that the birds were exposed to, and how often they were exposed to them. In addition, I used small earphones for delivery of altered auditory feedback to birds vocalizing in these operant experiments. In other words, I manipulated simple, individual variables and delivered precise feedback to these birds in order to better understand how sensory stimuli and sensory feedback might function in vocal learning.

The experiments described in this dissertation shed light on both the external and internal control of vocal production in budgerigars and give us a better understanding of how budgerigars learn contact calls. We know these birds learn new calls in a matter of weeks within small groups of vocalizing birds, but we don't know very much about the mechanisms underlying this process. For example, do they need to be in a social situation to learn or can isolated birds learn from other birds they can't see? What kinds of environmental stimuli elicit a specific call? Does call production depend on real-time auditory feedback? And do they learn the acoustic pattern of an entire call all at once or do they make small, piecemeal changes to call segments? Specifically, I address the following questions:

1. Do budgerigars show vocal learning (broadly defined to include contextual learning) based solely on auditory information?
2. What is the relative salience of visual versus acoustic stimuli in cueing vocal responses in these birds?
3. Are budgerigars sensitive to the level of auditory feedback?

4. Are budgerigars sensitive to the spectral and/or temporal pattern of auditory feedback?
5. Can budgerigars be driven to alter the pitch of their vocalizations?

The experiments in this dissertation answer these questions, provide new insights into budgerigar contact call learning and production, and set the stage for future investigations of the vocal control, vocal learning, and auditory feedback systems of this species and potential parallels with human behavior.

References

Banta Lavenex, P. (**2000**). "Lesions in the budgerigar vocal control nucleus nlc affect production, but not memory, of english words and natural vocalizations," Journal of Comparative Neurology 421, 437-460.

Baptista, L., and Petrinovich, L. (**1984**). "Social interaction, sensitive phases and the song template hypothesis in the white-crowned sparrow," Animal Behav. 32, 172-181.

Baptista, L. F., and Gaunt, L. L. (**1997**). "Interaction and vocal development in birds," in *Social influences on vocal development*, edited by C. T. Snowdon, and M. Hausberger (Cambridge University Press, Cambridge, England), pp. 23-40.

Baptista, L. F., and Schuchmann, K. L. (**1990**). "Song learning in the anna hummingbird (*calyptae anna*)," Ethology 84, 15-26.

Bauer, J. J., Mittal, J., Larson, C. R., and Hain, T. C. (**2006**). "Vocal responses to unanticipated perturbations in voice loudness feedback: An automatic mechanism for stabilizing voice amplitude," Journal of the Acoustical Society of America 119, 2363-2371.

Beecher, M. D., Stoddard, P. K., Campbell, S. E., and Horning, C. L. (**1996**). "Repertoire matching between neighbouring song sparrows," Animal Behaviour 51, 917-923.

Borden, G. J. (**1979**). "An interpretation of research of feedback interruption in speech," Brain Lang 7, 307-319.

Bottjer, S. W. (**2004**). "Developmental regulation of basal ganglia circuitry during the sensitive period for vocal learning in songbirds," in *Behavioral neurobiology* *of birdsong*, edited by H. P. Zeigler, and P. Marler (New York Academy of Sciences, New York), pp. 395-415.

Boughman, J. W. (**1998**). "Vocal learning by greater spear-nosed bats," Proceedings of the Royal Society of London B 265, 227-233.

Boughman, J. W., and Moss, C. F. (**2003**). "Social sounds: Vocal learning and development of mammal and bird calls," in *Acoustic communication, springer handbook of auditory research*, edited by A. M. Simmons, A. N. Popper, and R. R. Fay (Springer-Verlag, New York), pp. 138-224.

Brainard, M. S. (**2004**). "Contributions of the anterior forebrain pathway to vocal plasticity," in *Behavioral neurobiology of birdsong*, edited by H. P. Zeigler, and P. Marler (New York Academy of Sciences, New York), pp. 377-394.

Brainard, M. S., and Doupe, A. J. (**2000**). "Auditory feedback in learning and maintenance of vocal behaviour," Nature Reviews. Neuroscience 1, 31-40.

Brauth, S., Liang, W., Roberts, T. F., Scott, L. L., and Quinlan, E. M. (**2002**). "Contact call-driven zenk protein induction and habituation in telencephalic auditory pathways in the budgerigar (melopsittacus undulatus): Implications for understanding vocal learning processes," Learn Mem 9, 76-88.

Brauth, S. E., Heaton, J. T., Durand, S. E., Liang, W., and Hall, W. S. (**1994**). "Functional anatomy of forebrain auditory pathways in the budgerigar (melopsittacus undulatus)," Brain, Behavior And Evolution 44, 210-233.

Brenowitz, E. A., and Beecher, M. D. (**2005**). "Song learning in birds: Diversity and plasticity, opportunities and challenges," Trends Neurosci 28, 127-132.

Brittan-Powell, E. F., Dooling, R. J., and Farabaugh, S. M. (**1997**). "Vocal development in budgerigars (*melopsittacus undulatus*): Contact calls," J. Comp. Psychol. 111, 226-241.

Brockway, B. F. (**1964a**). "Ethological studies of the budgerigar (*melopsittacus undulatus*): Non-reproductive behavior," Behavior 22, 193-222.

Brockway, B. F. (**1964b**). "Ethological studies of the budgerigar (*melopsittacus undulatus*): Reproductive behavior," Behavior 23, 294-324.

Brockway, B. F. (**1969**). "Roles of budgerigar vocalization in the integration of breeding behavior," in *Bird vocalizations*, edited by R. A. Hinde (Cambridge University Press, London), pp. 131-158.

Brown, S. D., and Dooling, R. J. (**1992**). "Perception of conspecific faces by budgerigars (*melopsittacus undulatus*): I. Natural faces," J. Comp. Psychol. 106, 203-216.

Brown, S. D., and Dooling, R. J. (**1993**). "Perception of conspecific faces by budgerigars (*melopsittacus undulatus*): Ii. Synthetic models," J. Comp. Psychol. 107, 48-60.

Brown, S. D., Dooling, R. J., and O'Grady, K. (**1988**). "Perceptual organization of acoustic stimuli by budgerigars (*melopsittacus undulatus*): Iii. Contact calls," J. Comp. Psychol. 102, 236-247.

Burnett, T. A., Freedland, M. B., Larson, C. R., and Hain, T. C. (**1998**). "Voice f0 responses to manipulations in pitch feedback," J. Acoust. Soc. Am. 103, 3153-3161.

Clayton, D. F. (**2004**). "Songbird genomics : Methods, mechanisms, opportunities, and pitfalls," in *Behavioral neurobiology of birdsong*, edited by H. P. Zeigler, and P. Marler (New York Academy of Sciences, New York), pp. 45-60.

Cunningham, M. A., and Baker, M. C. (**1983**). "Vocal learning in white-crowned sparrows: Sensitive phases and song dialects," Behav Ecol Sociobiol 13, 259-269.

Cynx, J. (**1990**). "Experimental-determination of a unit of song production in the zebra finch (*taeniopygia guttata*)," J. Comp. Psychol. 104, 3-10.

Cynx, J., and Von Rad, U. (**2001**). "Immediate and transitory effects of delayed auditory feedback on bird song production," Anim. Behav. 62, 305-312.

Dave, A. S., and Margoliash, D. (**2000**). "Song replay during sleep and computational rules for sensorimotor vocal learning," Science 290, 812-816.

Deregnaucourt, S., Mitra, P. P., Feher, O., Maul, K. K., Lints, T. J., and Tchernichovski, O. (**2004**). "Song development: In search of the error signal," in *Behavioral neurobiology of birdsong*, edited by H. P. Zeigler, and P. Marler (New York Academy of Sciences, New York), pp. 364-376.

Dooling, R. J., Gephart, B. F., Price, P. H., McHale, C., and Brauth, S. E. (**1987**). "Effects of deafening on the contact calls of the budgerigar (*melopsittacus undulatus*)," Anim. Beh. 35, 1264-1266.

Dooling, R. J., Ryals, B. M., and Manabe, K. (**1997**). "Recovery of hearing and vocal behavior after hair-cell regeneration," Proc. Natl. Acad. Sci. USA 94, 14206-14210.

Doupe, A. J., and Kuhl, P. K. (**1999**). "Birdsong and human speech: Common themes and mechanisms," Annu. Rev. Neurosci. 22, 567-631.

Durand, S. E., Heaton, J. T., Amateau, S. K., and Brauth, S. E. (**1997**). "Vocal control pathways through the anterior forebrain of a parrot (melopsittacus undulatus)," The Journal Of Comparative Neurology 377, 179-206.

Elman, J. L. (**1981**). "Effects of frequency-shifted feedback on the pitch of vocal productions," J. Acoust. Soc. Am. 70, 45-50.

Farabaugh, S., and Dooling, R. J. (**1996**). "Acoustic communication in parrots: Laboratory and field studies of budgerigars, *melopsittacus undulatus*," in *Ecology and evolution of acoustic communication in birds*, edited by D. E. Kroodsma, and E. H. Miller (Cornell University Press, Ithaca, NY), pp. 97-118.

Farabaugh, S. M., Brown, E. D., and Dooling, R. J. (**1992**). "Analysis of warble song of the budgerigar, melopsittacus undulatus," Bioacoustics 4, 111-130.

Farabaugh, S. M., Linzenbold, A., and Dooling, R. J. (**1994**). "Vocal plasticity in budgerigars (*melopsittacus undulatus*): Evidence for social factors in the learning of contact calls," J. Comp. Psychol. 108, 81-92.

Franz, M., and Goller, F. (**2002**). "Respiratory units of motor production and song imitation in the zebra finch," J Neurobiol 51, 129-141.

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," J Comp Neurol 426, 182-196.

Gerhardt, H. C. (**1994**). "The evolution of vocalization in frogs and toads," Annual Review of Ecology and Systematics 25.

Glaze, C. M., and Troyer, T. W. (**2006**). "Temporal structure in zebra finch song: Implications for motor coding," Journal of Neuroscience 26, 991-1005.

Greenberg, S. (**1999**). "Speaking in shorthand: A syllable-centric perspective for understanding pronunciation variation," Speech Commun 29.

Guenther, F. H. (**2001**). "Neural modeling of speech production," in *Speech motor control in normal and disordered speech*, edited by B. Maassen, W. Hulstijn, R. Kent, H. F. M. Peters, and P. H. M. M. van Lieshout (Nijmegen, Uttgeverij Vantilt), pp. 12-15.

Gyger, M., Marler, P., and Pickert, R. (**1987**). "Semantics of an avian alarm call system - the male domestic-fowl, gallus-domesticus," Behav. 102, 15-40.

Hall, W. S., Brauth, S. E., and Heaton, J. T. (**1994**). "Comparison of the effects of lesions in nucleus basalis and field 'l' on vocal learning and performance in the budgerigar (melopsittacus undulatus)," Brain, Behavior And Evolution 44, 133-148.

Hausberger, M. (**1997**). "Social influences on song acquisition and sharing in the european starling *(sturnus vulgaris*)," in *Social influences on vocal development*, edited by C. T. Snowdon, and M. Hausberger (Cambridge University Press, Cambridge, England), pp. 128-156.

Heaton, J. T., and Brauth, S. E. (**1999**). "Effects of deafening on the development of nestling and juvenile vocalizations in budgerigars (*melopsittacus undulatus*)," J. Comp. Psychol. 113, 314-320.

Heaton, J. T., and Brauth, S. E. (**2000**). "Effects of lesions of the central nucleus of the anterior archistriatum on contact call and warble song production in the budgerigar (melopsittacus undulatus)," Neurobiol Learn Mem 73, 207-242.

Heaton, J. T., Dooling, R. J., and Farabaugh, S. M. (**1999**). "Effects of deafening on the calls and warble song of adult budgerigars (*melopsittacus undulatus*)," J. Acoust. Soc. Am. 105, 2010-2019.

Heaton, J. T., Farabaugh, S. M., and Brauth, S. E. (**1995**). "Effect of syringeal denervation in the budgerigar (melopsittacus undulatus): The role of the syrinx in call production," Neurobiology of Learning and Memory 64, 68-82.

Heinks-Maldonado, T. H., and Houde, J. F. (**2005**). "Compensatory responses to brief perturbations of speech amplitude," Acoustics Research Letters Online 6, 131-137.

Hile, A. G., Plummer, T. K., and Striedter, G. F. (**2000**). "Male vocal imitation produces call convergence during pair bonding in budgerigars, *melopsittacus undulatus*," Anim. Behav. 59, 1209-1218.

Hile, A. G., and Striedter, G. F. (**2000**). "Call convergence within groups of female budgerigars (*melopsittacus undulatus*)," Ethol. 106, 1105-1114.

Hough, G. E., and Volman, S. F. (**2002**). "Short-term and long-term effects of vocal distortion on song maintenance in zebra finches," Journal of Neuroscience 22, 1177-1186.

Howell, P. (**2002**). "The explan theory of fluency control applied to the treatment of stuttering by altered feedback and operant procedures," in *Current issues in* *linguistic theory: Pathology and therapy of speech disorders*, edited by E. Fava (John Benjamins, Amsterdam), pp. 95-118.

Howell, P., and Archer, A. (**1984**). "Susceptibility to the effects of delayed auditory feedback," Percept. & Psychophys. 36, 296-302.

Howell, P., and Sackin, S. (**2002**). "Timing interference to speech in altered listening conditions," Journal of the Acoustical Society of America 111, 2842-2852.

Hughes, M. S., Nowicki, S., and Lohr, B. (**1998**). "Call learning in black-capped chickadees (*parus atricapillus*): The role of experience in the development of 'chick-a-dee' calls," Ethology 104, 232-249.

Janik, V. M., and Slater, P. J. B. (**1997**). "Vocal learning in mammals," in *Advances in the study of behaviour*, edited by P. J. B. Slater, J. S. Rosenblatt, C. T. Snowdon, and H. Milinski (Academic Press, New York), pp. 59-99.

Janik, V. M., and Slater, P. J. B. (**2000**). "The different roles of social learning in vocal communication," Animal Behavior 60, 1-11.

Jarvis, E. D. (**2004**). "Learned birdsong and the neurobiology of human language," Ann Ny Acad Sci 1016.

Jarvis, E. D. (**2006**). "Selection for and against vocal learning in birds and mammals," Ornithol Sci 5, 5-14.

Jarvis, E. D., and Mello, C. V. (**2000**). "Molecular mapping of brain areas involved in parrot vocal communication," The Journal Of Comparative Neurology 419, 1-31.

Jones, G., and Ransome, R. D. (**1993**). "Echolocation calls of bats are influenced by maternal effects and change over a lifetime," Proceedings of the Royal Society of London B 252, 125-128.

Jürgens, U. (**1992**). "On the neurobiology of vocal communication," in *Nonverbal vocal communication*, edited by H. Papousek, U. Jürgens, and M. Papousek (Cambridge University Press, Paris), pp. 31-42.

Jürgens, U. (**1995**). "Neuronal control of vocal production in non-human and human primates," in *Current topics in primate vocal communication*, edited by E. Zimmerman, J. D. Newman, and U. Jürgens (Plenum Press, New York), pp. 199-206.

Jürgens, U. (**2002**). "Neural pathways underlying vocal control," Neurosci Biobehav R 26, 235-258.

Konishi, M. (**1963**). "The role of auditory feedback in the vocal behavior of the domestic fowl," Zeitschrift für Tierpsychologie 20, 349-367.

Konishi, M. (**1965a**). "Effects of deafening on song development in american robins and black-headed grosbeaks," Z Tierpsychol 22, 584-599.

Konishi, M. (**1965b**). "The role of auditory feedback in the control of vocalization in the white-crowned sparrow," Z Tierpsychol 22, 770-783.

Konishi, M. (**2004**). "The role of auditory feedback in birdsong," in *Behavioral neurobiology of birdsong*, edited by H. P. Zeigler, and P. Maler (New York Academy of Sciences, New York), pp. 463-475.

Kroodsma, D. E., and Konishi, M. (**1991**). "A suboscine bird (eastern phoebe, sayornis-phoebe) develops normal song without auditory-feedback," Animal Behav. 42, 477-487.

Kroodsma, D. E., and Miller, E. H. (**1982**). *Acoustic communication in birds* (Academic Press, New York, NY).

Lane, H., and Tranel, B. (**1971**). "Lombard sign and role of hearing in speech," Journal of Speech and Hearing Research 14, 677-709.

Lashley, K. S. (**1967**). "The problem of serial order in behavior," in *Cerebral mechanisms in behavior*, edited by L. A. Jeffress (Hafner, New York), pp. 112-146.

Lee, B. S. (**1950**). "Effects of delayed speech feedback," Journal of the Acoustical Society of America 22, 824-826.

Leonardo, A., and Konishi, M. (**1999**). "Decrystallization of adult birdsong by perturbation of auditory feedback," Nature 399, 466-470.

Lieberman, P. (**2002**). "On the nature and evolution of the neural bases of human language," Am J Phys Anthropol 45, 36-62.

Lombard, E. (**1911**). "Le signe de l'élévation de la voix," Ann. Maladies Oreille, Larynx, Nez, Pharynx 37, 101-119.

Lombardino, A. J., and Nottebohm, F. (**2000**). "Age at deafening affects the stability of learned song in adult male zebra finches," Journal of Neuroscience 20, 5054-5064.

Mammen, D. L., and Nowicki, S. (**1981**). "Individual-differences and within-flock convergence in chickadee calls," Behav Ecol Sociobiol 9, 179-186.

Manabe, K., and Dooling, R. J. (**1997**). "Control of vocal production in budgerigars (melopsittacus undulatus): Selective reinforcement, call differentiation, and stimulus control," Behav Process 41, 117-132.

Manabe, K., Dooling, R. J., and Brittan-Powell, E. F. (**2008**). "Vocal learning in budgerigars (*melapsittacus undulatus*): Effects of an acoustic reference on vocal matching," Journal of the Acoustical Society of America 123, 1729-1736.

Manabe, K., Kawashima, T., and Staddon, J. E. R. (**1995**). "Differential vocalization in budgerigars: Towards an experimental analysis of naming," J. Exp. Anal. Behav. 63, 111-126.

Manabe, K., Sadr, E. I., and Dooling, R. J. (**1998**). "Control of vocal intensity in budgerigars (*melopsittacus undulatus*): Differential reinforcement of vocal intensity and the lombard effect," J. Acoust. Soc. Am. 103, 1190-1198.

Manabe, K., Staddon, J. E. R., and Cleaveland, J. M. (**1997**). "Control of vocal repertoire by reward in budgerigars *(melopsittacus undulatus)*," Journal of Comparative Psychology 111, 50-62.

Margoliash, D. (**2002**). "Evaluating theories of bird song learning: Implications for future directions," J. Comp. Physiol. A 188, 851-866.

Marler, P. (**1970**). "A comparative approach to vocal learning - song development in white-crowned sparrows," J Comp Physiol Psych 71, 1-&.

Marler, P. (**1981**). "Birdsong: The acquisition of a learned motor skill," Trends In Neurosciences 4, 88-94.

Marler, P. (**2004**). "Bird calls: Their potential for behavioral neurobiology," in *Behavioral neurobiology of birdsong*, edited by H. P. Zeigler, and P. Marler (Annals of the New York Acedemay of Sciences, New York), pp. 31-44.

Marler, P., and Peters, S. (**1977**). "Selective vocal learning in a sparrow," Science 198, 519-521.

Mello, C. V. (**2002**). "Mapping vocal communication pathways in birds with inducible gene expression," J Comp Physiol A Neuroethol Sens Neural Behav Physiol 188, 943-959.

Miller, C. T., and Wang, X. (**2006**). "Sensory-motor interaction modulates a primate vocal behavior: Antiphonal calling in common marmosets," Journal of comparative physiology A 192, 27-38.

Mooney, R. (**2004**). "Synaptic mechanisms for auditory-vocal integration and the correction of vocal errors," Ann Ny Acad Sci 1016, 476-494.

Neilson, M. D., and Neilson, P. D. (**1991**). "Adaptive model theory of speech motor control and stuttering," in *Speech motor control and stuttering*, edited by H. G. M. Peters, W. Hulstijn, and C. W. Starkweather (Elsevier, Amsterdam), pp. 149-156.

Nelson, D. A. (**1997**). "Social interaction and sensitive phases for song learning: A critical review," in *Social influences on vocal development*, edited by C. T. Snowdon, and M. Hausberger (Cambridge University Press, Cambridge, England), pp. 7-22.

Nordeen, K., and Nordeen, E. (**1992**). "Auditory feedback is necessary for the maintenance of stereotyped song in adult zebra finches," Behavior. Neural. Biol. 57, 58-66.

Nordeen, K. W., and Nordeen, E. J. (**2004**). "Synaptic and molecular mechanisms regulating plasticity during early learning," in *Behavioral neurobiology of birdsong*, edited by H. P. Zeigler, and P. Marler (New York Academy of Sciences, New York), pp. 416-437.

Nottebohm, F. (**1972**). "Origins of vocal learning," Am Nat 106, 116-140.

Nottebohm, F. (**1999**). "The anatomy and timing of vocal learning in birds," in *The design of animal communication*, edited by M. D. Hauser, and M. Konishi (MIT Press, Cambridge, MA), pp. 63-110.

Nottebohm, F., and Nottebohm, M. E. (**1971**). "Vocalizations and breeding behav. Of surgically deafened ring doves (streptopelia risoria)," Anim Behav 19, 313-327.

Nottebohm, F., Stokes, T. M., and Leonard, C. M. (**1976**). "Central control of song in the canary, serinus canarius," J Comp Neurol 165, 457-486.

Okanoya, K., and Yamaguchi, A. (**1997**). "Adult bengalese finches (*lonchura striata* var. Domestica) require real-time auditory feedback to produce normal song syntax," J. Neurobiol. 33, 343-356.

Owings, D. H., and Leger, D. W. (**1980**). "Chatter vocalizations of california ground squirrels: Predator- and social-role specificity," Zeitschrift für Tierpsychologie 46.

Owings, D. H., and Virgina, R. A. (**1978**). "Alarm calls of california ground squirrels *(spermophilus beecheyi)*," Zeitschrift für Tierpsychologie 54.

Payne, R. B. (**1981**). "Song learning and social interaction in indigo buntings," Animal Behavior 29, 688-697.

Pepperberg, I. M. (**1993**). "A review of the effects of social interaction on vocal learning in african grey parrots *(psittacus erithacus)*," Neth J Zool 43, 104-124.

Plummer, T. K., and Striedter, G. F. (**2002**). "Brain lesions that impair vocal imitation in adult budgerigars," J Neurobiol 53, 413-428.

Price, P. (**1979**). "Developmental determinants of structure in zebra finch song," J. Comp. Physiol. Psych. 93, 260-277.

Richards, D. G., Wolz, J. P., and Herman, L. M. (**1984**). "Vocal mimicry of computer-generated sounds and vocal labeling of objects by a bottlenosed dolphin, tursiops truncatus," J. Comp. Psychol. 98, 10-28.

Riebel, K., and Todt, D. (**1997**). "Light flash stimulation alters the nightingale's singing style: Implications for song control mechanisms," Behaviour 134, 789-808.

Ringel, R. L., and Steer, M. D. (**1963**). "Some effects of tactile and auditory alterations on speech output," Journal of Speech and Hearing Research 6, 369-378.

Romand, R., and Ehret, G. (**1984**). "Development of sound production in normal, isolated, and deafened kittens during the first postnatal months," Developmental Psychobiology 17, 629-649.

Sakata, J. T., and Brainard, M. S. (**2006**). "Real-time contributions of auditory feedback to avian vocal motor control," The Journal Of Neuroscience: The Official Journal Of The Society For Neuroscience 26, 9619-9628.

Seyfarth, R. M., and Cheney, D. L. (**1986**). "Vocal development in vervet monkeys," Animal Behavior 34, 1640-1658.

Seyfarth, R. M., Cheney, D. L., and Marler, P. (**1980**). "Monkey responses to three different alarm calls: Evidence of predator classification and semantic communication," Science 210, 801-803.

Shipley, C., Buchwald, J. S., and Carterette, E. C. (**1988**). "The role of auditory feedback in the vocalizations of cats," Experimental Brain Research 69, 431-438.

Striedter, G. F. (**1994**). "The vocal control pathways in budgerigars differ from those in songbirds," J Comp Neurol 343, 35-56.

Striedter, G. F., Freibott, L., Hile, A. G., and Burley, N. T. (**2003**). "For whom the male calls: An effect of audience on contact call rate and repertoire in budgerigars, melopsittacus undulatus," Animal Behaviour 65, 875-882.

Summers, W. V., Pisoni, D. B., Bernacki, R. H., Pedlow, R. I., and Stokes, M. A. (**1988**). "Effects of noise on speech production: Acoustic and perceptual analyses," Journal of the Acoustical Society of America 84, 917-928.

Takahasi, M., Ikebuchi, M., and Okanoya, K. (**2005**). "Spatiotemporal properties of visual stimuli for song induction in bengalese finches," Neuroreport 16, 1339-1343.

Talmage-Riggs, G., Winter, P., Ploog, D., and Mayer, W. (**1972**). "Effect of deafening on the vocal behaviour of the squirrel monkey (saimiri sciureus). ," Folia Primatol 17, 404-420.

Tchernichovski, O., Mitra, P. P., Lints, T., and Nottebohm, F. (**2001**). "Dynamics of the vocal imitation process: How a zebra finch learns its song," Science 291, 2564-2569.

Thorpe, W. H. (**1958**). "The learning of song patterns by birds, with especial reference to the song of the chaffinch, *fringilla coelebs*," Ibis 100, 535-570.

Troyer, T. W., and Doupe, A. J. (**2000a**). "An associational model of birdsong sensorimotor learning i. Efference copy and the learning of song syllables," J. Neurophysiol. 84, 1204-1223.

Troyer, T. W., and Doupe, A. J. (**2000b**). "An associational model of birdsong sensorimotor learning ii. Temporal hierarchies and the learning of song sequence," J. Neurophysiol. 84, 1224-1239.

Vicario, D. S. (**2004**). "Using learned calls to study sensory-motor integration in songbirds. ," in *Behavioral neurobiology of birdsong*, edited by H. P. Zeigler, and P. Marler (New York Academy of Sciences, New York), pp. 246-262.

Wanker, R., and Fischer, J. (**2001**). "Intra- and interindividual variation in the contact calls of spectacled parrotlets *(forpus conspicillatus)*," Behaviour 138, 709-726.

West, M. J., and King, A. P. (**1988**). "Female visual displays affect the development of male song in the cowbird," Nature 334, 244-246.

Williams, H. (**2004**). "Birdsong and singing behavior," in *Behavioral neurobiology of birdsong*, edited by H. P. Zeigler, and P. Marler (New York Academy of Sciences, New York), pp. 1-30.

Woolley, S. M. N. (**2004**). "Auditory experience and adult song plasticity," in *Behavioral neurobiology of birdsong*, edited by H. P. Zeigler, and P. Marler (New York Academy of Sciences, New York), pp. 208-221.

Woolley, S. M. N., and Rubel, E. W. (**1997**). "Bengalese finches *lonchura striata* domestica depend upon auditory feedback for the maintenance of adult song," J. Neurosci. 17, 6380-6390.

Wright, T. F. (**1996**). "Regional dialects in the contact call of a parrot," P Roy Soc Lond B Bio 263, 867-872.

Wright, T. F., and Dorin, M. (**2001**). "Pair duets in the yellow-naped amazon (psittaciformes: *Amazona auropalliata*): Responses to playbacks of different dialects," Ethology 107, 111-124.

Wright, T. F., and Wilkinson, G. S. (**2000**). "Population genetic structure and vocal dialects in an amazon parrot," Proceedings of the Royal Society of London B 268, 609-616.

Wyndham, E. (**1980**). "Environment and food of the budgerigar (melopsittacus undulatus)," Australian Journal of Ecology 5, 47-61.

Yates, A. J. (**1963**). "Delayed auditory feedback," Psychol Bull 60, 213-232.

Zann, R. A. (**1990**). "Song and call learning in wild zebra finches in south-east australia," Animal Behavior 40, 818-828.

Zann, R. A. (**1996**). *The zebra finch: A synthesis of field and laboratory studies* (Oxford University Press, New York).

Zuberbühler, K. (**2000**). "Referential labeling in diana monkeys," Animal Behavior 59, 917-927.

Chapter 2 - External Control: Vocal Responses to Environmental Stimuli

I. INTRODUCTION

Both laboratory and field studies confirm the importance of social experience in songbird vocal learning (Baptista and Gaunt, 1997; Brenowitz and Beecher, 2005; Nelson, 1997; Williams, 2004). Many species require social interaction with live conspecifics to learn song, while others will learn from a model bird that they can interact with (Baptista and Petrinovich, 1984; Tchernichovski *et al.*, 2001; Zann, 1996). Social experience can drive learning so strongly, in fact, that some birds preferentially learn the song of heterospecifics that they can interact with, instead of conspecific song played through a loudspeaker (Baptista and Petrinovich, 1984; Payne, 1981) .

Vocal learning in songbirds occurs within a complex, interactive social milieu and depends on a suite of environmental stimuli, including both auditory and visual information. However, little attention has historically been paid to the specific pairings between these sensory stimuli and the vocalizations they elicit (Nelson, 1997). There are some exceptions: Studies show that sparrows preferentially learn songs containing their own species-specific acoustic patterns (Marler and Peters, 1977), song sparrows produce particular song-types based on the song-types produced by territorial neighbors (Beecher *et al.*, 1996), male singing behavior is elicited by the sight of females in many songbird species (Takahasi *et al.*, 2005; Zann, 1996) and female cowbirds signal to singing males a preference for specific song types through rapid wing movements and postural displays (West and King, 1988).

Thus, both acoustic and visual stimuli elicit vocalizations in songbirds, but in general the precise stimulus features that trigger vocal behavior are incompletely known.

Social experience also plays a critical role in parrot vocal learning (e.g., Farabaugh and Dooling, 1996; Pepperberg, 1993; Wright, 1996; Wright and Dorin, 2001; Wright and Wilkinson, 2000). Budgerigars (*Melopsittacus undulatus*) are small Australian parrots with a well-studied, learned vocal repertoire (see review in Farabaugh and Dooling, 1996). They live in large, social flocks and interact with each other in a dynamic, reciprocal manner. Learning in these birds occurs during changes in social settings, especially during the addition and removal of flockmates (Brown *et al.*, 1988; Farabaugh *et al.*, 1994; Hile *et al.*, 2000; Hile and Striedter, 2000; Striedter *et al.*, 2003).

Evidence shows that budgerigars do not learn from conspecifics that they can only hear, although they do learn from cagemates that they can interact with (Brittan-Powell *et al.*, 1997; Farabaugh *et al.*, 1994; Hile and Striedter, 2000). One caveat in these studies showing a lack of learning in budgerigars based solely on auditory experience is that none of the studies analyzed calls using a detailed, fine-grained analysis of call parameters such as average frequency or duration and so may have overlooked potential evidence for learning. There is reason to believe that budgerigars can learn based on auditory information alone, since we know that they attend to the acoustic structure of calls when other sensory information is not present. For example, budgerigars discriminate individuals based solely on hearing their contact calls in psychoacoustic tests (Brown *et al.*, 1988) and they respond more to their mate’s call than they do to the calls of other budgerigars during playback experiments (Ali *et al.*, 1993).

Here, we wanted to further examine the question of whether budgerigars show vocal learning based solely on auditory information by performing a more detailed analysis of vocalizations produced during calling bouts between visually-isolated birds. We defined vocal learning broadly to include contextual learning – in which different vocalizations are elicited by different stimuli or contexts (Boughman and Moss, 2003; Janik and Slater, 1997, 2000). Budgerigars commonly vocalize to one another over long distances and out of sight of each other during calling bouts (Farabaugh and Dooling, 1996) and studying this behavior can help clarify the role of external sensory feedback in the production and control of vocal behavior, especially if individuals respond to each others’ vocal signals by altering the timing, pattern and/or acoustic structure of particular call-types (e.g., Falls, 1992; Miller and Wang, 2006; Todt and Naguib, 2000).

To this end, we recorded the vocal behavior of budgerigar pairs that were housed individually and out of sight of each other over a twelve week period. Birds were placed in separate acoustic isolation chambers during recording sessions and so could only use auditory information from their vocal partner to guide their own vocal productions. Each bird’s vocal repertoire was analyzed to see whether they showed evidence of vocal learning broadly defined. Specifically, we hypothesized that: 1) budgerigars would respond to particular calls produced by a vocal partner with a specific call-type of their own, and 2) over time, budgerigars would show changes in the acoustic parameters (e.g., average frequency, duration, etc.) of their calls both within and across sessions.

II. EXPERIMENT 1: AN ANALYSIS OF VOCAL REPERTOIRES DURING CALLING BOUTS

A. Methods

1. Subjects

The subjects in this experiment were four adult budgerigars (3 male, 1 female). Each bird was separately caged and had *ad libitum* access to both food and water.

B. Procedure

1. Recording Procedure

Budgerigars were housed separately in their home cages throughout this study. They were therefore not able to interact socially with their vocal partner, although they could still hear each other. Birds were recorded as pairs – a male-male pair (Pair 1) and a male-female pair (Pair 2). The same birds were recorded together throughout the experiment. That is, the birds constituting Pair 1 and those constituting Pair 2 were always the same birds in every recording session. Approximately every two weeks, each pair was housed individually in an acoustic isolation chamber (Industrial Acoustic Company model AC-1) for several hours. Observations in our laboratory suggest that budgerigars kept in isolation are more likely to vocalize. After several hours, the doors of the chambers were opened and a directional Audio-Technica Carotoid microphone (PRO35A) was aimed at each animal's cage. Microphones were attached to a Marantz solid state digital recorder (PMD670) and each bird's vocal behavior was stored on a separate channel of a PCM WAV file at a sampling rate of 48 kHz. The birds were allowed to interact acoustically, but not visually, from inside their chambers and were returned to their home cages after approximately 100-200 calls were recorded from each bird. Pairs were recorded six times across a twelve-week period (one recording session occurred approximately every two weeks).

Call Segmentation and Call Typing

All analysis programs were generated using MATLAB software and Tucker Davis Technologies (TDT) System III hardware (Gainesville, FL). Each recording session was transferred from the Marantz digital recorder to computer after the session. A MATLAB program then segmented each WAV file into its component contact calls. This program advanced through each WAV file and selected acoustic signals that exceeded both a user-defined value for minimum intensity (based on the overall amplitude of the recording) and for minimum duration. Each selected signal was presented both acoustically and visually (as a spectrogram) to a rater familiar with budgerigar contact calls who then either accepted or rejected the signal as a call. All contact calls were saved in a separate file along with a log file detailing the segment start time and end time for further analysis.

Next, a multidimensional scaling (MDS) algorithm was used to determine how many call-types were in each bird's repertoire. A spectral cross-correlation program generated a similarity index between all calls produced in a session. This program created a spectrogram for each signal using a 256-point Hanning window with 50% window overlap. These spectrograms were then compared using a MATLAB 2-dimensional cross correlation algorithm (MATLAB function XCORR2).

This algorithm generated a series of correlation values representing all possible temporal offsets between the two spectrograms. The maximum correlation value was taken as the similarity index between the two calls. A matrix of similarity values was constructed from all calls produced in a test session and was analyzed using a MATLAB classical multidimensional scaling algorithm (MATLAB function MDSCALE). Calls in the 2-dimensional space created from the MDS output clustered into separate groups by call-type (see Figure 1 for an example). Spectrograms were examined from each cluster before being classified and labeled as a particular call-type. A small percentage of calls (<5%) were not clearly assigned to a particular cluster by the MDS program because of the presence of extraneous background sounds, such as wing flapping or cage noise. These calls were assigned to a cluster manually by a rater familiar with each bird's call-types.

Finally, the center call from every cluster in each bird's first recording session was stored and used as a call-type exemplar. Thus, each bird had a set of two calls representing each of its call-type clusters. These two exemplars were then compared to all calls produced by the bird in subsequent sessions and used to categorize those calls.

Repertoire Analysis

All signals classified as contact calls were analyzed in the following way: First, we gathered the start and end times of all the contact calls (derived from the log file created when the original WAV files were segmented into separate contact calls - see above) produced by each bird in a session. For each call, we then measured the delay between the end of that call and the start of the next call by the partner (the

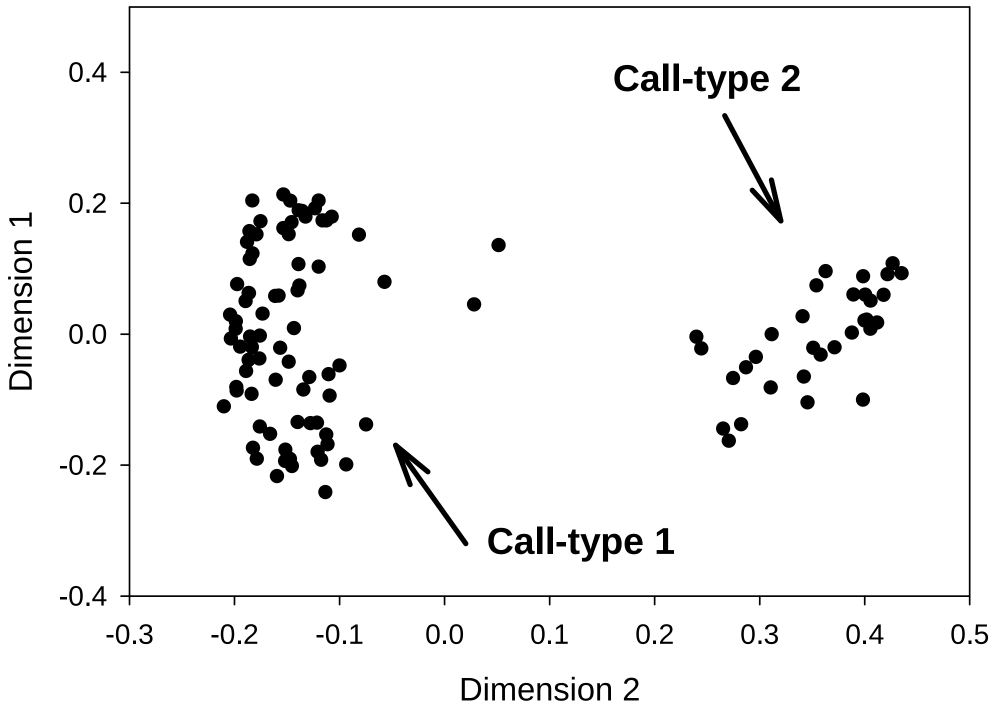

Figure 1. MDS output showing calls grouping into two clusters based on call-type. Assignment to a particular call-type was used to determine whether birds responded to the calls of a vocal partner with a specific call of their own.

partners' call was only considered a response if it occurred before a subsequent call from the first bird). We then used the call-type labels assigned by the MDS program to each of those calls in order to determine whether a particular call-type in one bird were responded to with a specific call-type in the other bird.

Finally, all vocalizations produced during the experiment were stored digitally and analyzed off-line using a MATLAB signal analysis program. Analysis involved: 1) generation of power spectra iteratively across each call in 5 ms windows (with 50% window overlap), 2) measurement of several acoustic parameters from these power spectra, including average peak frequency and 3 dB bandwidth of the spectral peak, and 3) calculation of whole-call measurements, including Wiener entropy (a unitless measure of disorder, see Tchernichovski *et al.*, 2001) and a similarity measure of that call's exemplar (see above for a description of how exemplars were chosen). Statistics were performed on these measures using SPSS software. Also, peak frequency contours were saved for each call to facilitate comparisons within and between sessions.

C. Results and Discussion of Experiment 1

All birds vocalized readily in the current experiment. The average number of contact calls produced in a session was 153 +/- 55 calls. Almost all calls were produced in the context of calling bouts. The majority of calls (63.1%) produced by an individual during calling bouts were given within 0.5 seconds of the end of the partner's call. Each bird produced two call-types. One bird produced a third call-type, but this call-type was not included in the present analyses because it occurred rarely (i.e., it represented < 5% of all calls from this bird and occurred in just two out of the six recording sessions). We labeled each bird's dominant call (i.e., the call-type produced most-often) from session 1 as call-type 1 and the non-dominant call as call-type 2. Across all four birds, call-type 1 was produced more often than call-type 2 throughout all six recording sessions (Mean = 64.7% vs. 35.3%, SD = +/-5.64%).

Budgerigars did not respond to particular calls produced by their vocal partner by producing a specific call-type of their own. The proportion of call-types produced in response to a partner's vocalizations did not differ as a function of which call-types the partner produced (Paired-samples t-test; t(23) = -.481, p = .635) and did not differ from proportion of call-types produced overall in the entire session (Call-type 1: Paired-samples t-test; t(23) = -.436, p = .667, Call-type 2: Paired-samples t-test; t(23) = -1.07, p = .298). Thus, birds always tended to produce their dominant call-type regardless of the call-type produced by the other bird.

Interestingly, the latency to respond was always significantly shorter for one individual (0.48 +/- 0.12 s) than for its partner (1.42 +/- 0.22 s). The same individual within a pair always showed this shorter latency and the temporal relationship between birds was preserved across recording sessions. This measure of asymmetry in call timing between pair members that is similar to the 'leader/follower' relationship first described by Smith and Norman (1979) in red-winged blackbirds. Blackbirds with a higher perceived threat level showed a shorter latency to respond during vocal interactions.

There were no changes in call acoustic parameters within a session for either call-type 1 or call-type 2 across birds. A paired-samples t-test showed no significant differences between calls produced in the first half of a session and calls produced in the second half of a session for any of the acoustic parameters we measured – similarity to exemplar, average frequency, 3 dB bandwidth, duration, or Wiener entropy (see Table 1). There was also no difference in the proportion of call-types produced between the first and second half of a session (Table 1). Repeated-measures ANOVA showed a significant difference over sessions in both similarity to exemplar and average frequency, although this effect only occurred in call-type 2 (the non-dominant call); there were no significant differences over sessions in any of the remaining acoustic parameters for call-type 2 (Table 2). There were no significant changes in any acoustic parameters over sessions for call-type 1 (Table 2).

These results show that a bird's dominant call (call-type 1) remains relatively fixed over time during these calling bouts and that a bird's non-dominant call (call-type 2) is more plastic and shows variation in structure over time. This change was measured as an average decrease in call frequency over sessions across all birds (average frequency in session 1: 2929.6 +/- 78.2 Hz; session 6: 2814.1 +/- 46.9 Hz) and a concomitant decrease in similarity to exemplar (average similarity in session 1: r = 0.70 +/- 0.04; session 2: r = 0.54 +/- 0.09). This change in frequency does not appear to reflect call convergence between members of a pair. Paired-samples t-tests showed that the non-dominant calls of each pair did not become more similar between the first and last sessions (Pair 1: $\underline{t}(23) = 0.60$, $\underline{p} = 0.55$; Pair 2: $\underline{t}(30) = -0.16$, $\underline{p} = 0.88$). It is noteworthy that this decrease in frequency does not appear to occur across an entire call. Instead, call segments toward the end of a call tend to be reduced in frequency relative to segments toward the beginning of a call (see Figure 2 for an example).

Table 1. Changes in Call Parameters Within a Session During Calling Bouts

	Call-type I		Call-type II	
Acoustic Measures	**t(5)**	**Significance**	**t(5)**	**Significance**
Butter				
Correlation	0.42	0.69	-0.07	0.95
Average Frequency	0.57	0.59	1.09	0.33
3 dB Bandwidth	-0.20	0.85	-0.92	0.40
Duration	1.52	0.19	1.08	0.33
Wiener Entropy	1.30	0.25	2.34	0.07
Repertoire %	-0.35	0.74	0.35	0.74
Lewis				
Correlation	-0.24	0.82	0.01	0.99
Average Frequency	1.73	0.14	2.09	0.09
3 dB Bandwidth	-0.71	0.51	-0.80	0.46
Duration	-0.55	0.61	1.86	0.12
Wiener Entropy	1.41	0.22	0.94	0.39
Repertoire %	-0.03	0.98	0.03	0.98
Cosmo				
Correlation	1.20	0.28	0.79	0.46
Average Frequency	-0.67	0.53	-0.50	0.64
3 dB Bandwidth	-0.92	0.40	-0.36	0.74
Duration	0.62	0.56	0.91	0.41
Wiener Entropy	0.63	0.56	0.71	0.51
Repertoire %	1.15	0.30	-1.15	0.30
Grace				
Correlation	1.10	0.32	2.44	0.06
Average Frequency	0.03	0.98	-0.59	0.58
3 dB Bandwidth	-1.10	0.32	-0.81	0.46
Duration	0.52	0.63	-0.38	0.72
Wiener Entropy	2.39	0.06	1.64	0.16
Repertoire %	-0.24	0.82	0.24	0.82

Table 2. Changes in Call Parameters Across Sessions During Calling Bouts

	Call-type I		**Call-type II**	
Acoustic Measures	**F (5,15)**	**Significance**	**F(5,15)**	**Significance**
Correlation	0.32	0.89	**8.55**	**< 0.01**
Average Frequency	2.05	0.13	**9.46**	**< 0.01**
3 dB Bandwidth	2.14	0.12	0.43	0.82
Duration	1.85	0.16	2.62	0.07
Wiener Entropy	1.23	0.34	0.86	0.53
Repertoire %	2.16	0.11		

Measures in **BOLD** are significantly different across sessions

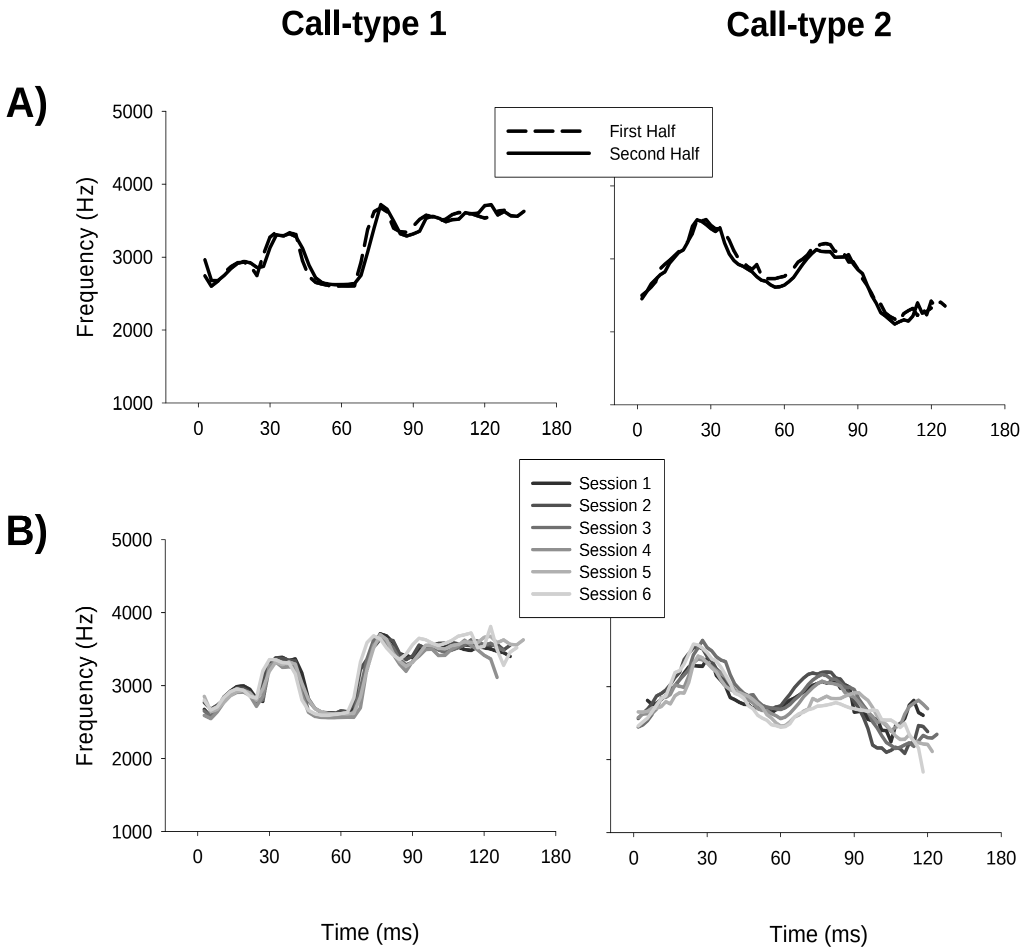

Figure 2. Average frequency contours of a dominant and non-dominant call produced by one bird during a calling bout. Frequency contours from both call-types show no changes in frequency structure in calls within a session (row A).There are also no differences seen across sessions in call-type 1 (the bird's dominant call), but there are significant changes seen in the contours of call-type 2 (the bird's non-dominant call) over the six recording sessions. These changes occur primarily in the latter segments of the call.

Figure 2 shows average frequency contours from each call-type (call-type 1: left column; call-type 2: right column) of one of the birds in this study both within sessions (row A) and across sessions (row B). Changes are only seen across sessions and only in call-type 2 (i.e., right column, row B). These changes are seen as a general flattening of a terminal segment of the contour.

These results show that budgerigars closely coordinate the timing of their vocal behavior with that of a vocal partner in a naturalistic environment, but they do not alter their call-types. Also, birds do not adjust the acoustic characteristics of their dominant call-type during calling bouts but do make changes to their non-dominant call-types. Given that both bird pairs showed a similar decrease in frequency over time, it is possible that this change is not the result of any vocal learning process but, instead, reflects a passive drifting in frequency or more simple maturational factors that are particular to non-dominant calls and which operate independently of social interaction.

III. GENERAL INTRODUCTION FOR OPERANT EXPERIMENTS

Budgerigars learn contact calls socially, engage in calling dialogues with conspecifics, and learn most readily from birds they can see and interact with (e.g., Brittan-Powell *et al.*, 1997; Farabaugh and Dooling, 1996; Farabaugh *et al.*, 1994; Hile *et al.*, 2000; Hile and Striedter, 2000; Striedter *et al.*, 2003). Results from Experiment 1 confirm and extend these findings, showing that budgerigars do not use call-types from a vocal partner to guide their own vocal behavior. However, this raises the question of how these birds respond to specific environmental stimuli with a specific vocal response.

Budgerigars must process and integrate sensory stimuli when selecting appropriate vocal responses during imitative vocal learning, but the relative contributions of these different stimuli to that process are impossible to tease apart in a natural context. Operant conditioning techniques provide a way to disentangle the salience of the complex cues for learning by allowing the experimenter to control stimulus characteristics and associations in a way that would be impossible in more naturalistic studies. Salience here means those stimulus attributes that are most conspicuous and/or prominent to the animal in forming sensory-vocal associations. There is a long history of animal work showing that certain stimuli are preferred for learning or are easier to associate with particular behavioral responses than others. Often, these easier associations are those with an underlying ethological significance (for a review, see Marler *et al.*, 1980). For example, swamp sparrows preferentially learn conspecific song instead of song sparrow song (Marler and Peters, 1977) and honeybees associate odors with food more easily than colors (in Marler *et al.*, 1980; Menzel, 1985).

Budgerigar vocal behavior is easily brought under control in an operant environment with differential reinforcement using simple visual stimuli. Here we use such reinforcement to drive vocal learning and plasticity in these birds (Manabe and Dooling, 1997; Manabe *et al.*, 2008; Manabe *et al.*, 1995). We used differential reinforcement to train birds to produce a particular contact call to visual (LEDs) and/or auditory stimuli (contact calls/tones) that differed either in spatial location (left vs. right) or stimulus features (i.e., visual = color; auditory = call-type/tone frequency). The goal is to examine the relative saliency of visual and auditory stimulus cues when the associated response is vocal production.

IV. GENERAL METHODS FOR OPERANT EXPERIMENTS

A. Subjects

The subjects in these experiments were four adult budgerigars from a colony maintained in an aviary at the University of Maryland. Each bird was separately caged and had *ad libitum* access to water. Since food was used to reinforce vocal behavior, the birds were maintained at 90% of their free-feeding body weight. The University of Maryland Animal Care and Use Committee approved all experimental procedures.

B. Apparatus

Birds were trained in an operant testing apparatus consisting of a small wire cage (14 cm x 12 cm x 17 cm) constructed of wire mesh and mounted in an acoustic isolation chamber (Industrial Acoustic Company model AC-1). Three light-emitting diodes (left, center, and right LEDs) were attached to a piece of anechoic foam on the front panel of the cage at approximately the level of the bird's head. Three small speakers (SONY model MDR-Q22LP) were mounted on the exterior of the cage – one at the center above the front LED panel and one on each of the left and right sides. A small directional microphone (SONY model ECM-77B), located just below the LED panel, detected vocalizations. A food hopper containing hulled millet was located on the floor of the cage under the front LED panel. A small video camera was used to monitor the bird's behavior while in the chamber. See Figure 3 for an image of this operant setup.

C. Training/Testing Procedure and Analysis

Figure 3. Image of a subject behaving in the operant chamber. Birds are trained to vocalize to an illuminated LED (located just in front of and above the bird's head in the photograph). Vocalizations are detected by a microphone (located just below the LED) and compared to a stored template of the bird's call. If the call matches the template (i.e., exceeds a user-defined correlation value), then the bird is rewarded with access to food (via the raising of a food hopper located below the cage floor – seen as blue in the picture). Refer to the text for a more complete description of this operant setup.

1. Contact Call Detection & Analysis

Training/testing and analysis programs were generated using MATLAB software and Tucker Davis Technologies (TDT) System III hardware (Gainesville, FL). The output of the microphone was amplified, low-pass filtered at 10 kHz, and sent to a circular memory buffer in a TDT real-time digital signal processor (RP2.1) at a nominal sampling rate of 25 kHz. A typical budgerigar contact call has a duration of 100-150 milliseconds and spectral energy concentrated between 2-4 kHz (Farabaugh and Dooling, 1996; Farabaugh *et al.*, 1998; Farabaugh *et al.*, 1994). Therefore, incoming signals were classified as a contact calls if signal intensity exceeded a user-defined value for a minimum of 70 milliseconds and if, during this time, the signal power in the frequency band between 2 and 4 kHz exceeded that measured between 4 and 10 kHz.

2. Initial Training (Shaping)

Birds were first habituated to the experimental chamber and trained to eat from the food hopper when it was activated. Once the birds consistently ate from the raised hopper, manual shaping of vocalizations began. Here, typical aviary sounds were played in the operant chamber to induce the birds to vocalize. Whenever the birds responded to the aviary tape with a contact call, the experimenter activated the hopper. Birds quickly came to associate vocalizing in the test chamber with access to food and, therefore, tape playback was phased out over several training sessions. When birds reliably produced contact calls in the absence of the aviary tape, vocal behavior was reinforced automatically.

Birds were next trained to vocalize only when the center LED was illuminated. Here, the LED turned off each time a vocalization was acquired and turned on again after a random time interval (approximately 5-15 seconds). Only vocalizations produced when the light was illuminated were reinforced. Vocalizations produced when the LED was turned off caused the random interval timer to reset and increased the wait time before the LED turned back on. Birds successfully completed this phase of training when they reliably vocalized in the chamber both without the flock tape and only in response to the illuminated center LED.

3. Contact Call Recognition

After completing the previous phase, birds were tested in several further training sessions to establish a call repertoire. The most typical contact call in a bird's repertoire was selected as that bird's "template" call (see Manabe and Dooling, 1997). A spectral cross-correlation program generated a similarity index between all calls produced in these sessions. This program created a spectrogram for each signal using a 256-point Hanning window with 50% window overlap. These spectrograms were then compared using a MATLAB 2-dimensional cross correlation algorithm (MATLAB function XCORR2). This algorithm generated a series of correlation values representing all possible temporal offsets between the two spectrograms. The maximum correlation value was taken as the similarity index between the two calls. This similarity index was then normalized so that it was zero if two calls were perfectly dissimilar and one if the calls were identical. A matrix of similarity values was constructed from all calls produced in a test session and was analyzed using a MATLAB classical multidimensional scaling algorithm. The call in the center of the largest cluster in this two-dimensional space was selected as the template call for the next phase of training.

4. Template Training (Precision)

Subsequent training sessions used this template call in order to differentially reinforce vocal behavior. Birds were rewarded only for producing calls that were similar to the template call (using the same spectral cross-correlation algorithm described above). Every vocalization produced by a bird was compared to the stored digital template in real-time. The bird was reinforced if the correlation between the two calls exceeded a user-defined value. No reward was given if the correlation did not exceed this value. At first, the criterion was set very low (e.g., r = .01) so that all calls were reinforced. The criterion was then gradually increased over several sessions to a maximum value of r = .70. All training sessions were terminated after 50 reinforcements or 25 minutes, whichever came first. Subjects were tested in two daily sessions, five days per week. All test sessions were separated by at least three hours.

V. EXPERIMENT 2: EFFECTIVENESS OF VISUAL VERSUS AUDITORY STIMULI IN CUING A VOCAL RESPONSE

A. Methods

1. Subjects

Four adult budgerigars (3 males, 1 female) were used in this experiment.

B. Procedure

Once the birds were trained to asymptotic levels of performance on the template-training task described above, a new testing phase was introduced in which budgerigars were trained to produce two different contact calls using a 1-back procedure similar to that described by Manabe and colleagues (e.g., Manabe *et al.*, 1997). Briefly, this procedure rewards birds for producing contact calls that are different from the previously-produced call (i.e., the correlation between the two calls did not exceed a user-defined r value) and successful completion of this task results in birds producing at least two call-types. The two most commonly-produced calls from each bird were stored as templates and birds were trained to produce a particular call when presented with a specific visual or auditory cue in a series of testing conditions. These conditions were:

A. Visual stimuli – Location difference. Cues were compound audio-visual stimuli consisting of two spatially-separated (i.e., left and right) LEDs and playback of one of the two template calls (i.e., Template A + LED A / Template B + LED B). Call playback occurred through the center speaker above the center panel of the operant cage. Birds were required to produce a particular call when presented with a specific compound stimulus.

B. Visual stimuli – Quality difference. The cue was a single LED that alternated between the colors red and green. A correct response required a subject to pair a particular color with a specific vocal response. No auditory stimuli were presented in this experiment.

C. Auditory stimuli – Location difference. Here the auditory cue was playback of the birds' own two call templates. Call stimuli were presented through the two speakers located on either side of the operant cage 180° apart. One template was always presented from the right speaker and the other template was always presented from the left speaker. A correct response required a subject to pair a particular acoustic cue (i.e., Template A + Left

Speaker / Template B + Right Speaker) with a specific vocal response. Because the acoustic stimulus is the same call that the bird is required to produce, the bird only needed to repeat what it heard in order to make a correct response. No visual stimuli were presented in this experiment.

D. Auditory stimuli – Quality difference. The cue was playback of one of two different auditory stimuli (i.e., two tone stimuli [2 kHz and 4 kHz] or two contact call stimuli) through the center speaker above the operant cage center panel. A correct response required a subject to pair a particular auditory stimulus with a specific vocal response. In the latter case, the birds' two stored templates were the auditory stimuli. As in Experiment 2C, the acoustic stimuli were the same calls the birds were required to produce and, therefore, they only needed to repeat what they heard in order to make a correct response. No visual stimuli were presented in this experiment.

Each cue condition (A-D) required the bird to complete a series of training sessions followed by 10 test sessions. This occurred as follows: Stimulus presentation initially proceeded sequentially during training on these tasks. Birds were presented with the same stimulus (either visual or auditory and either a quality or a location difference) on successive trials until a correct response was given. Correct responses were followed by a switch to the other stimulus, which was then presented on successive trials until the bird again produced the correct vocalization. Stimulus presentation continued in this manner until a bird's percent correct for a given session exceeded 80%. At that time, the two stimuli were randomly presented during 10 additional test sessions. This random presentation ensured that the animals were attending to the stimulus features when choosing a response and not simply learning to alternate between call-types. Performance was assessed based on the number of sessions required to reach 80% criterion during sequential presentation and percent correct from sessions in which stimulus presentation was random. Each session consisted of 50 reinforced trials (all calls were compared to the subject's stored call templates), and each trial was composed of one cue presentation and one vocal response by the animal.

C. Results and Discussion of Experiment 2

Results from each of the four cue conditions were as follows:

A. Visual stimuli – Location difference. All four birds learned to produce a particular contact call to each of the two compound stimuli during sequential presentation. The average number of sessions needed to reach criterion was 15 +/- 3 sessions. Performance was maintained at or above this level throughout all 10 sessions of random stimulus presentation (Percent correct: 80.1% +/- 1.1%) (Figure 4A). These results show that budgerigars can learn to associate different vocalizations with particular audio-visual compound stimuli in an operant environment.

B. Visual stimuli – Quality difference. All four birds learned to produce a particular contact call to each of two visual stimuli during sequential presentation. The average number of sessions needed to reach criterion was 11 +/- 8 sessions. Performance was maintained at or above this level throughout all 10 sessions of random stimulus presentation (percent correct: 84.5% +/- 1.9%) (Figure 4B). These results show that budgerigars can learn to associate different vocalizations with different visual stimuli originating from the same

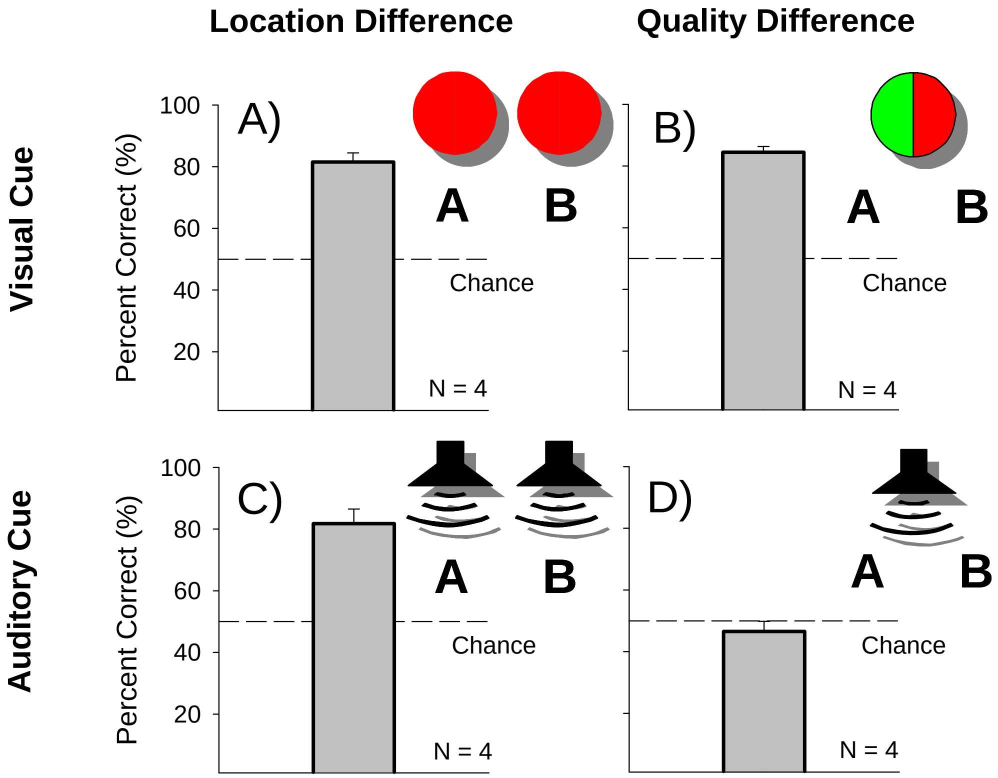

Figure 4. Strength of learning associations between particular contact calls and environmental stimuli in an operant environment. Budgerigars were trained to produce particular contact calls to specific auditory and visual stimuli in order to examine which stimuli these animals use when making vocal responses. These birds easily learn to associate different calls with location differences among visual stimuli (Panel A). Location was manipulated using two LEDs that were spatially separated (e.g., left LED = call-type 1/right LED = call-type 2). Similarly, different calls can be associated with quality differences among visual stimuli (Panel B). Here, one centrally-located LED was alternated between the colors red and green (e.g., red LED = call-type 1/green LED = call-type 2). Birds were also able to learn associations with acoustic stimuli differing in location (Panel C). Two speakers were hung outside of the testing cage and contact call stimuli were played to the bird (contact call stimulus A = call-type 1/contact call stimulus B = call-type 2). However, birds were unable to learn associations with acoustic stimuli differing in quality (panel D). Here, either contact call stimuli or tones were played through a single, centrally-located speaker (stimulus A = call-type 1/stimulus B = call-type 2).

location in an operant environment.

C. Auditory stimuli – Location difference. All four birds learned to produce a particular contact call to each of the two auditory stimuli during sequential presentation. The average number of sessions needed to reach criterion was 9 +/- 5 sessions. Performance was maintained at or above this level throughout all 10 sessions of random stimulus presentation (Percent correct: 81.8% +/- 4.7%) (Figure 4C). These results show that budgerigars can learn to associate different vocalizations with different, spatially-separated auditory stimuli in an operant environment.

D. Auditory stimuli – Quality difference. The subjects could not learn to produce different contact calls to different auditory stimuli (Figure 4D). Testing was terminated after 28 sessions for all birds after two subjects stopped behaving in the operant chamber. Overall performance remained at chance levels across all sessions (average percent correct: 46.6% +/- 3.3%; maximum percent correct across all subjects: 61.4%). Neither contact calls (percent correct: 42.4 +/- 5.0%) nor tone stimuli (percent correct: 50.7 +/- 5.3%) were sufficient for these birds to make a correct discrimination.

Overall, these results show that associations between visual stimuli and vocal production are easier to learn than are associations between auditory stimuli (including vocalizations) and vocal production. In some ways, this finding is consistent with results from Experiment 1 in a free calling context where birds did not change the characteristics of their contact call during a vocal dialogue with another bird. But in other ways, these results are surprising because of the remarkable failure by the birds to learn to produce a particular call in response to a specific auditory cue. Recall that budgerigars learn the calls of other birds presumably by listening to them calling. Even more remarkable is the fact that the birds failed to learn an auditory-vocal association even when the call stimuli were the birds' own vocalizations. In other words, the birds were able to reproduce the signals they heard (i.e. their own vocalizations), but could not associate them with an auditory cue (again, their own vocalizations). Obviously birds were able to both produce and perceive the differences between their own vocalizations but they could not make the association. These results point to a kind of disconnect between the production and perception mechanisms in these birds reminiscent of conduction aphasia in humans – the inability to repeat what is heard.

VI. EXPERIMENT 3: RELATIVE SALIENCE OF AUDITORY AND VISUAL STIMULI AS CUES TO VOCAL PRODUCTION

Previous experiments showed that budgerigars can produce different contact calls to spatially-separated audio-visual compound stimuli and spatially-separated auditory-only stimuli. Here we look at the relative salience of visual vs. auditory stimuli in learning these associations by removing the visual component of the audio-visual compound stimuli (Experiment 3A). We also look at the relative salience of quality vs. location cues when learning associations with auditory-only stimuli (Experiment 3B).

A. Methods

1. Subjects

Three budgerigars (1 male, 2 female) from Experiment 2 were used in this experiment.

B. Procedure

A. Relative salience of auditory vs. visual stimuli. We tested the relative salience of the auditory component of the audio-visual compound stimuli from Experiment 2A by removing the visual stimulus once the animals had reached criterion performance. This was accomplished by either turning both LEDs on or turning both LEDs off during stimulus presentation. Subjects had to rely on the auditory component alone in order to produce the correct response. Birds were run in 5 sessions for each removal condition. Sessions consisted of 50 reinforced trials (all calls were compared to the subject's stored call template) and each trial was composed of one auditory stimulus and one vocal response by the animal.

B. Relative salience of auditory quality vs. auditory location cues. Subjects in this experiment were trained in two conditions: They were presented with playback of either two of their own call templates (as in Experiment 2C) or the call templates of another subject in the experiment. Each subject completed both call stimulus conditions in a pseudorandom order. Birds were required to produce a particular call when presented with a particular playback call. In the situation where the acoustic stimulus is the same call that the bird is required to produce, the bird only needs to repeat what it hears in order to make a correct response. In the other case, the bird must produce calls that match their own templates when presented with another bird's calls.

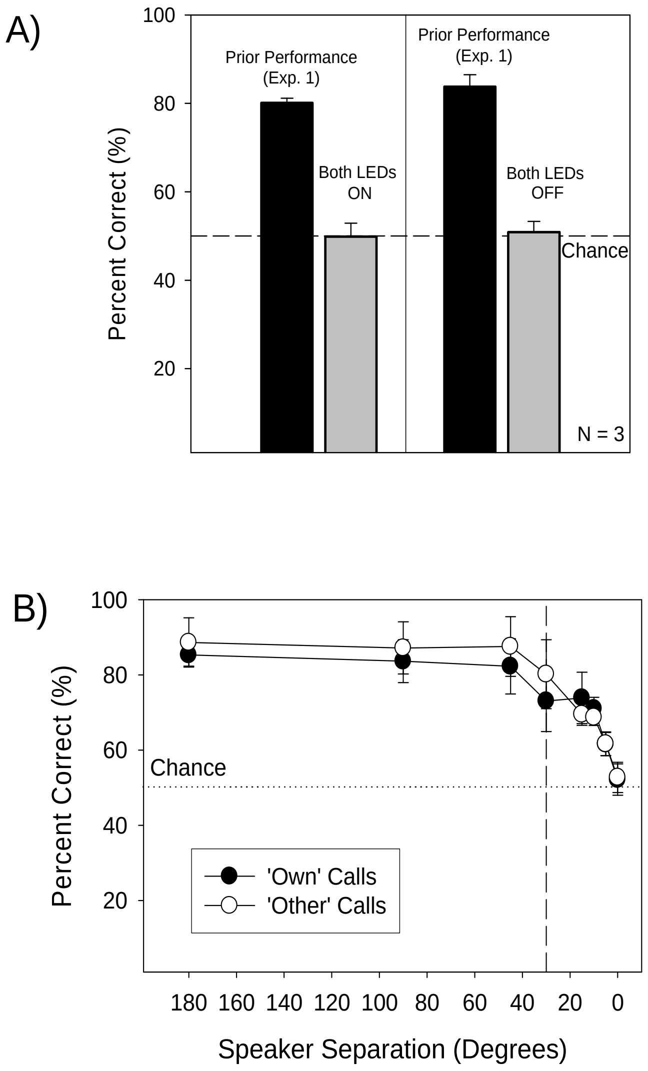

Figure 5. Relative salience of visual versus auditory stimuli as cues to vocal production. A) Experiment 2A showed that budgerigars can learn to associate vocalizations with different audio-visual compound stimuli. After similar training in Experiment 3 (black bars), performance drops to chance levels following removal of the visual stimulus as a response cue (LEDs ON/LEDs OFF). Thus, budgerigars had only learned the visual part of the stimulus when learning the task; the auditory stimulus was largely ignored. B) Effects of manipulating speaker position on the learned associations between auditory location cues and vocal responses in Experiment 2C. The two speakers lose their salience as separate cues at about 15-30° separation, which is the typical threshold for discriminating azimuth in budgerigars.

All stimuli were presented to the birds from one of two small speakers (SONY model MDR-Q22LP) which were hung from a semicircular stand positioned around the front exterior of the testing cage. Speakers were level with the height of the subjects' head and speaker position was varied along the azimuthal plane of this stand (at 180°, 90°, 45°, 30°, 15°, 10°, 5°, and 0° increments where 0° was directly in front of the bird). Birds were run in 2 sessions for each azimuthal position. Sessions consisted of 50 reinforced trials (all calls were compared to the subject's stored call template) and each trial was composed of one auditory stimulus and one vocal response by the animal.

C. **Results and Discussion of Experiment 3**

A. Relative salience of auditory vs. visual stimuli. Performance for all three birds dropped to chance levels under both visual stimulus removal conditions. Average percent correct with both LEDs on was 49.9% +/- 3.0% (Figure 5A, left panel) and 50.9% +/- 2.4% with both LEDs off (Figure 5A, right panel). Thus, the birds had learned only the visual stimulus and did not attend to the auditory stimulus when learning the task in Experiment 2A. Although the three birds appear unable to use an auditory stimulus to guide their choice of call-type, they still used it as cue to vocalize. Subjects withheld vocalizing until they heard the call playback and responded to the auditory stimulus by producing a contact call in response.

B. Relative salience of auditory quality vs. auditory location cues. Performance for all three birds dropped to chance levels as the speaker position was moved from 180° to 0° regardless of whether the birds were presented with playback of their own calls (180° separation = 85.3% +/- 3.0%; 0° separation = 52.9% +/- 4.2%) or the calls of another bird (180° separation = 88.6% +/- 6.7%; 0° separation = 52.7% +/- 4.0%) (Figure 5B). In both cases, performance declined most rapidly as the speaker position was moved to < 30° separation. This finding is supported by previous sound discrimination data showing that budgerigars discriminate differences in azimuth poorly at angles under 30° (Park and Dooling, 1991) and suggests that these birds had learned only the speaker position and not the auditory stimulus.

VII. EXPERIMENT 4: EFFECTIVENESS OF AUDITORY STIMULUS QUALITY IN CUING VOCAL PRODUCTION IN A MULTIPLE-BIRD ACOUSTIC BACKGROUND

Budgerigars normally produce and learn contact calls out of sight of each other in a loud flock environment containing several birds calling simultaneously. Thus, vocal behavior typically occurs in the presence of competing acoustic stimuli and birds that engage in vocal interactions in such an environment have to call loudly in order to be heard over the calling of many other birds. This raises the possibility that acoustic competition may be a key component in focusing attention on a specific auditory-vocal association. In this case, birds may attend more to the precise acoustic features of their vocal partner’s calls and try to mimic aspects of those calls in order to maintain a dialogue. To recreate this context in the current experiment, we presented auditory stimuli over a background of budgerigar flock noise. All other aspects of the present experiment were the same as in the quiet during Experiment 2.

A. Methods

1. Subjects

Three adult budgerigars (1 male, 2 female) from Experiment 3 were used in this experiment.

B. Procedure

Subjects were presented with three different auditory cue stimulus sets: Tones (either 2 kHz or 4 kHz - within the range of best hearing for these animals), the bird's own template calls, and the template calls of another subject in the experiment. All stimuli were played through the center speaker above the center panel of the operant cage. No visual stimuli were presented in this experiment. After completing one stimulus set, a bird was immediately moved on to the next stimulus set. Each bird moved through the stimulus sets in a pseudo-random order.

The experiment proceeded in four stages for each stimulus set. The first stage was a single test session that was methodologically identical to Experiment 2D. Birds were presented with the same auditory stimulus on successive trials until a correct response was given. Correct responses were followed by a switch to the other acoustic stimulus, which was presented until the bird produced the correct vocalization. In stage 2, each bird ran four additional test sessions with a sequential stimulus presentation. A recording of the flock at the University of Maryland was played during these sessions through an additional, larger speaker (Realistic, Catalog # 40-1289) located just behind the front LED panel of the test cage at a level of approximately 55-60 dB SPL. All birds were familiar with the flock sounds. In stage 3, testing alternated between the two flock tape conditions (present / absent) for an additional 9 sessions with sequential stimulus presentation. This 3 stage paradigm was repeated for all three auditory stimulus types. Finally, each of the three stimulus types were randomly assigned to a final nine sessions (three sessions per stimulus type, one stimulus type per session) in which the flock tape was always used. Stimuli were randomly presented in these sessions. All sessions consisted of 50 reinforced trials (all calls were compared to the subject's stored call template) and each trial was composed of one auditory cue and one vocal response by the animal.

C. Results and Discussion of Experiment 4

All of the birds showed an increase in performance as a result of exposure to the flock tape for all three stimulus sets (Figure 6). As in Experiment 2D, performance in stage 1 was at chance levels for all three stimulus types. However, birds improved immediately during stage 2 and continued to show improvement across the four sessions in which the flock tape was played, regardless of stimulus type other calls. Performance remained above chance levels throughout stage 3 (i.e. alternating sessions in which the flock tape was present/absent) and during stage 4 (i.e., randomized sessions). Repeated-measures ANOVA showed that performance improved significantly across all stages as a result of the flock tape for all three stimulus sets ('Own' calls: $\underline{F}(6,12) = 14.3$, $\underline{p} < 0.01$; 'Other' calls: $\underline{F}(6,12) = 15.8$, $\underline{p} < 0.01$; Tones: $\underline{F}(6,12) = 3.71$, $\underline{p} < 0.05$). Importantly, paired-samples t-tests showed that performance was significantly higher in the stage 3 quiet sessions compared to the initial quiet sessions for contact call stimuli ('Own' calls: $\underline{t}(2) = -6.12$, $\underline{p} < 0.05$; 'Other' calls: $\underline{t}(2) = -6.63$, $\underline{p} < 0.05$) but not for tones ($\underline{t}(2) = 3.46$, $\underline{p} = 0.07$). That is, these birds appear to require the flock tape to acquire, but not to maintain, the associations reported in this experiment – at least for contact call stimuli.

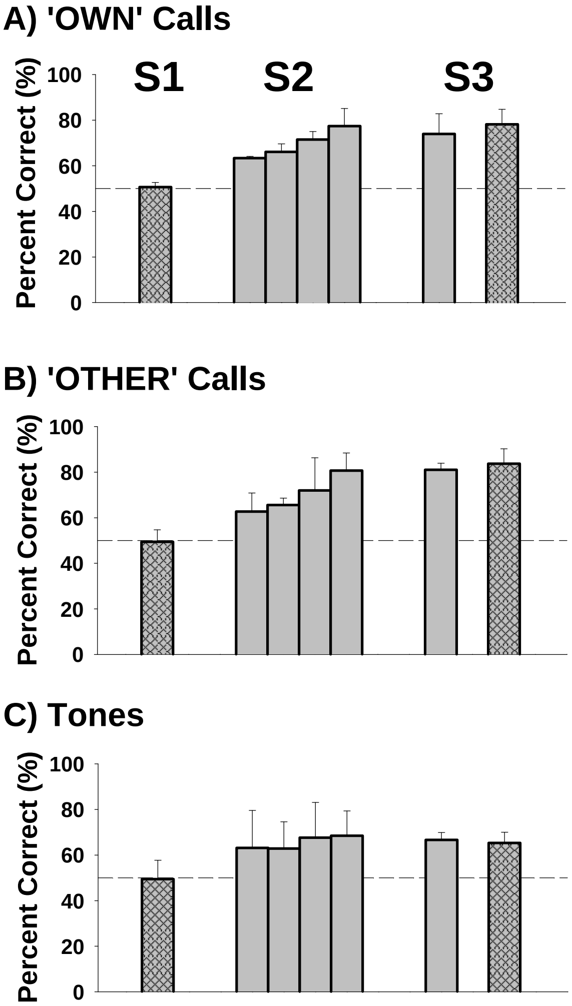

Figure 6. Effect of a 'natural background' context on learning auditory location cues. Experiment 2D showed that birds were unable to produce particular calls to either contact call stimuli or tones when all stimuli were played through a single, centrally-located speaker. This task, however, becomes easy to learn when performed while a recording of calling birds is played in the background. We tested birds using their own calls (A), another bird's calls (B), and pure tones (C) as acoustic stimuli. Birds initially performed at chance levels during stage 1 (S1), but playing a flock tape for 4 sessions during stage 2 (S2) results in an immediate improvement in performance. After exposure to the flock tape, birds were run in a third stage comprised of 9 additional sessions in which the flock tape alternated on/off (S3). Here performance was the same regardless of whether the flock tape was used or not. Interestingly, this learning did not transfer between stimulus sets. Birds always began a new stimulus set performing at chance levels. Hatched bars are sessions with a quiet background and non-hatched bars are sessions with the flock tape as background.

Interestingly, this learning did not transfer between stimulus sets. Birds always began a new stimulus set performing at chance levels. These results offer intriguing evidence that there is a kind of social facilitation in budgerigar vocal production and vocal learning. Stimulus-response associations successfully learned by birds in the current experiment were not learned in Experiment 2D. The only difference between the two experiments is the playback of a budgerigar flock tape in the present experiment. This strongly suggests that there may be mechanisms which prevent budgerigars from learning new calls outside of a normal, socially-rich environment when only auditory cues are present.

VIII. GENERAL DISCUSSION

These experiments show that budgerigars do not easily form associations between auditory information and a particular vocal output. Birds did not show changes in the acoustic parameters of their dominant call-type during calling bouts. We did measure a significant decrease in call frequency (and a concomitant decrease in similarity to a call exemplar) in their non-dominant call-type. This was not call convergence as measured by spectral cross-correlation. Also, the decrease did not occur across an entire call, but instead occurred primarily in a small segment of a call. No other parameters had changed in the non-dominant call-type. Also, budgerigars did not use call-types from a partner to guide their own productions. They did closely coordinate the timing of their vocal behavior with that of their partner in a ‘leader/follower’ relationship.

In an operant situation, birds learned to produce specific contact calls to different spatially-separated visual stimuli different-colored visual stimuli arising from the same location, and spatially-separated acoustic stimuli. However, they did not learn to associate a particular vocal response with different auditory stimuli coming from the same location even when the stimulus and the response were the same (i.e. the bird's own contact call). Budgerigars typically vocalize in loud flocks where multiple birds are calling simultaneously, and so we next presented these same stimuli within an acoustic background of vocalizing birds. Performance improved in this more 'natural' context.

In sum, these experiments extend previous findings in both natural and operant environments that describe a kind of social facilitation in budgerigar contact call learning (Brittan-Powell *et al.*, 1997; Farabaugh *et al.*, 1994; Hile *et al.*, 2000; Hile and Striedter, 2000; Manabe *et al.*, 2008; Striedter *et al.*, 2003), and may reflect a limitation on call learning in these birds. A central tenet of classical learning theory is that any arbitrary stimulus can be associated, through learning, with any arbitrary response, though there is now a wealth of information on sensory biases and learning constraints which soften this argument (e.g., Bolles, 1973; Garcia *et al.*, 1974; Hinde and Hinde, 1973). One of these constraints involves stimulus and response attributes in auditory discrimination tasks. In general, simple auditory discriminations take significantly longer to learn – up to an order of magnitude longer - using two-choice procedures than the same task takes using go/no go procedures (Burdick, 1979; Dobrzecka *et al.*, 1966; Lawicka, 1968). Miller and colleagues have proposed a general learning principle based on these findings, the "quality-location hypothesis", which states that stimulus quality (e.g., tone vs. noise) is easily associated with response quality (i.e., presence/absence) and stimulus location (e.g., left vs. right) is easily associated with response location (i.e., go right vs. go left) but not vice versa (Bowe *et al.*, 1987; Miller and Bowe, 1982).

Sensory biases and learning constraints are known to exist in the vocal production and perception of songbirds and budgerigars (Brittan-Powell *et al.*, 1997; Dooling and Searcy, 1980; Dooling *et al.*, 1990; Marler and Peters, 1977; Nelson and Marler, 1993; Okanoya and Dooling, 1991). The present findings fit into the more general body of research describing biological constraints on auditory discrimination learning and provide another example of learning limitations in budgerigars. The failure of these birds to learn an auditory-vocal association, and the ease with which they can learn a visual-vocal association, under quiet conditions is remarkable given that these birds, and parrots in general, are such accomplished vocal learners.

Finally, these results suggest that temporal coordination of calls is more important than production of specific call-types in establishing vocal interactions between visually-isolated individuals. These data raise two important questions: What is the purpose of call-sharing in this species if call-types are not used in these vocal interactions, and what does the precise timing of calls communicate between individuals during interactions? The most obvious explanation for call-sharing is that call-types represent badges of group membership (Boughman and Moss, 2003; Farabaugh and Dooling, 1996; Farabaugh *et al.*, 1994; Janik and Slater, 1997; Treisman, 1978). Contact calls are used primarily in the formation and maintenance of social bonds and call plasticity is associated with changes to an individual's social environment (Brittan-Powell *et al.*, 1997; Farabaugh and Dooling, 1996; Farabaugh *et al.*, 1994; Hile *et al.*, 2000; Hile and Striedter, 2000; Manabe *et al.*, 2008; Striedter *et* *al.*, 2003). Birds housed together learn to produce a common flock call through call convergence (Farabaugh *et al.*, 1994; Hile and Striedter, 2000) and pre-existing similarities in call structure may function in mate choice (Moravec *et al.*, 2006). Thus, shared calls provide a means of highlighting a bird's place within a larger social network – as a member of a specific flock or a member of a specific mated pair - and may provide a means of integrating new members into those networks.

The relevance of the timing differences that we report between individuals during vocal interactions remains an open question. There is a possibility that timing carries no intrinsic meaning to these birds and, instead, is simply an epiphenomenon associated with the rapid rate of responses between individuals (usually < 0.5 sec). However, the fact that the 'leader/follower' roles were preserved between individuals and across recording sessions suggests that the birds had taken on a specific role based on some difference between the individuals. Work in songbirds has focused on two potential explanations for this kind of difference in call timing: Differences in internal state or condition between individuals, as in nightingales (Naguib, 1999), ovenbirds (Popp, 1989), and red-winged blackbirds (Smith and Norman, 1979), or differences in social status, as in nightingales (Naguib *et al.*, 1999) (for a review, see Todt and Naguib, 2000). We noted no apparent differences between birds in condition or status a priori. Future work will need to explicitly test these hypotheses.

Acknowledgments

We thank Elizabeth Brittan-Powell and Peter Marvit for comments on the manuscript. We also thank Leah Dickstein for help in performing the experiments.

This work was supported by NIH grant DC-00198 to RJD, NIH grant DC-04664 to RJD, & NIH grant DC-006766 to MSO.

References

Ali, N. J., Farabaugh, S., and Dooling, R. (**1993**). "Recognition of contact calls by the budgerigar (*melopsittacus undulatus*)," B Psychonomic Soc 31, 468-470.

Baptista, L. F., and Gaunt, L. L. (**1997**). "Interaction and vocal development in birds," in *Social influences on vocal development*, edited by C. T. Snowdon, and M. Hausberger (Cambridge University Press, Cambridge, England), pp. 23-40.

Baptista, L. F., and Petrinovich, L. (**1984**). "Social interaction, sensitive phases and the song template hypothesis in the white-crowned sparrow," Animal Behav. 32, 172-181.

Bolles, R. C. (**1973**). "The comparative psychology of learning: The selective association principle and some problems with 'general' laws of learning," in *Perspectives in animal behavior*, edited by G. Bermant (Scott, Foresman and Co., Glenview, IL).

Boughman, J. W., and Moss, C. F. (**2003**). "Social sounds: Vocal learning and development of mammal and bird calls," in *Acoustic communication, springer handbook of auditory research*, edited by A. M. Simmons, A. N. Popper, and R. R. Fay (Springer-Verlag, New York), pp. 138-224.

Bowe, C. A., Miller, J. D., and Green, L. (**1987**). "Qualities and locations of stimuli and responses affecting discrimination learning of chinchillas (chinchilla laniger) and pigeons *(columba livia)*," Journal of Comparative Psychology 101, 132-138.

Brenowitz, E. A., and Beecher, M. D. (**2005**). "Song learning in birds: Diversity and plasticity, opportunities and challenges," Trends Neurosci 28, 127-132.

Brittan-Powell, E. F., Dooling, R. J., and Farabaugh, S. M. (**1997**). "Vocal development in budgerigars (*melopsittacus undulatus*): Contact calls," J. Comp. Psychol. 111, 226-241.

Brown, S. D., Dooling, R. J., and O'Grady, K. (**1988**). "Perceptual organization of acoustic stimuli by budgerigars (*melopsittacus undulatus*): Iii. Contact calls," J. Comp. Psychol. 102, 236-247.

Burdick, C. K. (**1979**). "The effect of behavioral paradigm on auditory discrimination learning: A literature review," Journal of Audiology Research 19, 59-82.

Dobrzecka, C., Szwejkowska, G., and Konorski, J. (**1966**). "Qualitative versus directional cues in two forms of differentiation," Science 153, 87-89.

Dooling, R., and Searcy, M. (**1980**). "Early perceptual selectivity in the swamp sparrow," Dev. Psychobiol. 13, 499-506.

Dooling, R. J., Brown, S. D., Park, T. J., and Okanoya, K. (**1990**). "Natural perceptual categories for vocal signals in budgerigars (*melopsittacus undulatus*)," in *Comparative perception*, edited by W. C. Stebbins, and M. A. Berkley (John Wiley & Sons, New York), pp. 345-373.

Falls, J. B. (**1992**). "Playbacks: A historical perspective," in *Playback and studies of animal communication*, edited by P. K. McGregor (Plenum Press, New York), pp. 11-33.

Farabaugh, S., and Dooling, R. J. (**1996**). "Acoustic communication in parrots: Laboratory and field studies of budgerigars, *melopsittacus undulatus*," in *Ecology and evolution of acoustic communication in birds*, edited by D. E. Kroodsma, and E. H. Miller (Cornell University Press, Ithaca, NY), pp. 97-118.

Farabaugh, S. M., Dent, M. L., and Dooling, R. J. (**1998**). "Hearing and vocalizations in native australian budgerigars (melopsittacus undulatus)," J. Comp. Psychol. 112, 74-81.

Farabaugh, S. M., Linzenbold, A., and Dooling, R. J. (**1994**). "Vocal plasticity in budgerigars (*melopsittacus undulatus*): Evidence for social factors in the learning of contact calls," J. Comp. Psychol. 108, 81-92.

Garcia, J., Hankins, W. G., and Rusiniak, K. W. (**1974**). "Behavioral regulation of the milieu interne in man and rat," Science 185, 824-831.

Hile, A. G., Plummer, T. K., and Striedter, G. F. (**2000**). "Male vocal imitation produces call convergence during pair bonding in budgerigars, *melopsittacus undulatus*," Anim. Behav. 59, 1209-1218.

Hile, A. G., and Striedter, G. F. (**2000**). "Call convergence within groups of female budgerigars (*melopsittacus undulatus*)," Ethol. 106, 1105-1114.

Hinde, R. A., and Hinde, J. (eds). (**1973**). *Constraints on learning: Limitations and predispositions* (Academic Press, New York).

Janik, V. M., and Slater, P. J. B. (**1997**). "Vocal learning in mammals," in *Advances in the study of behaviour*, edited by P. J. B. Slater, J. S. Rosenblatt, C. T. Snowdon, and H. Milinski (Academic Press, New York), pp. 59-99.

Janik, V. M., and Slater, P. J. B. (**2000**). "The different roles of social learning in vocal communication," Animal Behavior 60, 1-11.

Lawicka, W. (**1968**). "Differring effectiveness of auditory quality and location cues in two forms of differentiation learning," Acta Biologiae Experimentalis 29, 83-92.

Manabe, K., Cleaveland, M. J., and Staddon, J. E. R. (**1997**). "Control of vocal repertoire by reward in budgerigars (*melopsittacus undulatus*)," J. Comp. Psychol. 111, 50-62.

Manabe, K., and Dooling, R. J. (**1997**). "Control of vocal production in budgerigars (melopsittacus undulatus): Selective reinforcement, call differentiation, and stimulus control," Behav Process 41, 117-132.

Manabe, K., Dooling, R. J., and Brittan-Powell, E. F. (**2008**). "Vocal learning in budgerigars (*melapsittacus undulatus*): Effects of an acoustic reference on vocal matching," Journal of the Acoustical Society of America 123, 1729-1736.

Manabe, K., Kawashima, T., and Staddon, J. E. R. (**1995**). "Differential vocalization in budgerigars: Towards an experimental analysis of naming," J. Exp. Anal. Behav. 63, 111-126.

Marler, P. R., Dooling, R. J. and Zoloth, S. (**1980**). "Comparative perspecitves on ethology and behavioral development," in *Comparative methods in psychology*, edited by M. H. Bornstein (Lawrence Erlbaum Associates, New Jersey), pp. 189-230.

Marler, P., and Peters, S. (**1977**). "Selective vocal learning in a sparrow," Science 198, 519-521.

Menzel, R. (**1985**). "Learning in honeybee in an ecological and behavioural context," in *Experimental & behavioural ecology*, edited by M. Lindauer and B. Hölldobler (Stuttgart: Fischer), pp. 195-205.

Miller, C. T., and Wang, X. (**2006**). "Sensory-motor interaction modulates a primate vocal behavior: Antiphonal calling in common marmosets," Journal of comparative physiology A 192, 27-38.

Miller, J. D., and Bowe, C. A. (**1982**). "Roles of the qualities and locations of stimuli and responses in simple associative learning: The quality-location hypothesis," Pavlovian Journal of Biological Science 17, 129-139.

Moravec, M. L., Striedter, G. F., and Burley, N. T. (**2006**). "Assortative pairing based on contact call similarity in budgerigars, melopsittacus undulatus," Ethology 112, 1108-1116.

Naguib, M. (**1999**). "Effects of song overlapping and alternating on nocturnally singing nightingales," Animal Behaviour 58, 1061-1067.

Naguib, M., Fichtel, C., and Todt, D. (**1999**). "Nightingales respond more strongly to vocal leaders of simulated dyadic interactions," Proceedings of the Royal Society of London B 266, 537-542.

Nelson, D. A. (**1997**). "Social interaction and sensitive phases for song learning: A critical review," in *Social influences on vocal development*, edited by C. T. Snowdon, and M. Hausberger (Cambridge University Press, Cambridge, England), pp. 7-22.

Nelson, D. A., and Marler, P. (**1993**). "Innate recognition of song in white-crowned sparrows - a role in selective vocal learning," Animal Behav. 46, 806-808.

Okanoya, K., and Dooling, R. J. (**1991**). "Perception of distance calls by budgerigars (melopsittacus-undulatus) and zebra finches (poephila-guttata) - assessing species-specific advantages," J. Comp. Psychol. 105, 60-72.

Park, T. J., and Dooling, R. J. (**1991**). "Sound localization in small birds: Absolute localization in azimuth," J. Comp. Psychol. 105, 125-133.

Payne, R. B. (**1981**). "Song learning and social interaction in indigo buntings," Animal Behavior 29, 688-697.

Pepperberg, I. M. (**1993**). "A review of the effects of social interaction on vocal learning in african grey parrots *(psittacus erithacus)*," Neth J Zool 43, 104-124.

Popp, J. W. (**1989**). "Temporal aspects of singing interactions among territorial ovenbirds *(seiurus aurocapillus)*," Ethology 82, 127-133.

Smith, D. G., and Norman, D. O. (**1979**). "Leader-follower' singing in red-winged blackbirds," Condor 81, 83-84.

Striedter, G. F., Freibott, L., Hile, A. G., and Tyler Burley, N. (**2003**). "For whom the male calls: An effect of audience on contact call rate and repertoire in budgerigars, *melopsittacus undulatus*," Anim. Behav. 65, 875-882.

Takahasi, M., Ikebuchi, M., and Okanoya, K. (**2005**). "Spatiotemporal properties of visual stimuli for song induction in bengalese finches," Neuroreport 16, 1339-1343.

Tchernichovski, O., Mitra, P. P., Lints, T., and Nottebohm, F. (**2001**). "Dynamics of the vocal imitation process: How a zebra finch learns its song," Science 291, 2564-2569.

Todt, D., and Naguib, M. (**2000**). "Vocal interactions in birds: The use of song as a model in communication," in *Advances of the study of behavior*, edited by P. J. B. Slater, J. S. Rosenblatt, C. T. Snowdon, and T. J. Roper (Academic Press, New York), pp. 247-296.

Treisman, M. (**1978**). "Bird song dialects, repertoire size, and kin association," Anim. Behav. 26, 814-817.

West, M. J., and King, A. P. (**1988**). "Female visual displays affect the development of male song in the cowbird," Nature 334, 244-246.

Williams, H. (**2004**). "Birdsong and singing behavior," in *Behavioral neurobiology of birdsong*, edited by H. P. Zeigler, and P. Marler (New York Academy of Sciences, New York), pp. 1-30.

Wright, T. F. (**1996**). "Regional dialects in the contact call of a parrot," P Roy Soc Lond B Bio 263, 867-872.

Wright, T. F., and Dorin, M. (**2001**). "Pair duets in the yellow-naped amazon (psittaciformes: *Amazona auropalliata*): Responses to playbacks of different dialects," Ethology 107, 111-124.

Wright, T. F., and Wilkinson, G. S. (**2000**). "Population genetic structure and vocal dialects in an amazon parrot," Proceedings of the Royal Society of London B 268, 609-616.

Zann, R. A. (**1996**). *The zebra finch: A synthesis of field and laboratory studies* (Oxford University Press, New York).

Chapter 3 - Internal Control: I. The Lombard and Fletcher Effects.

I. INTRODUCTION

Animals that learn their vocalizations rely on auditory feedback for the development and maintenance of a normal vocal repertoire (for reviews, see Boughman and Moss, 2003; Doupe and Kuhl, 1999; Farabaugh and Dooling, 1996; Janik and Slater, 1997, 2000). Human speech, for example, depends on feedback mechanisms that regulate vocal amplitude (for a review, see Lane and Tranel, 1971; Lombard, 1911). One such phenomenon, the Lombard effect, describes an increase in vocal amplitude in response to an increase in ambient noise level (for a review, see Lane and Tranel, 1971). Other vocal changes include increases in syllable duration and vocal pitch and decreases in speaking rate (Draegert, 1951; Dreher and O'Neill, 1958; Hanley and Steer, 1949). The Fletcher effect, a related phenomenon, describes a decrease in vocal amplitude in response to an increase in perceived vocal loudness (Lane and Tranel, 1971; Siegel and Pick, 1974). These responses maintain a constant signal-to-noise ratio in vocal output across a range of ambient noise levels and therefore function to preserve speech intelligibility in varied listening conditions.

Signal degradation due to environmental noise is a problem for any animal acoustic communication system. Mechanisms of noise-dependent amplitude changes in vocal behavior similar to the Lombard effect have been described in monkeys (Sinnott *et al.*, 1975), quail (Potash, 1972), hummingbirds (Pytte *et al.*, 2003), songbirds (Brumm and Todt, 2002; Cynx *et al.*, 1998; Kobayashi and Okanoya, 2003), and budgerigars (Manabe *et al.*, 1998). Technical limitations prevent these animal studies from precisely controlling either subjects' behavior or feedback delivery compared to human work. For example, animals were tested while freely vocalizing (see Manabe *et al.*, 1998 for an exception to this), which prevented strict control over the specific time and type of vocalizations produced. Also, noise feedback was delivered to subjects in the free-field, thereby complicating acoustical analyses of vocalizations and comparisons between noise levels.

There have been no studies of the Fletcher effect in nonhuman animals primarily due to the difficulties associated with presenting temporally-aligned, amplitude-scaled feedback to a freely-vocalizing animal. Headphones would be required to ensure that subjects perceive the feedback as its own vocal output and not simply as an additional signal interfering with its own vocalizations. This type of control is extremely difficult to accomplish with freely-behaving animals. Thus, previous research on this phenomenon could not be conducted with the kind of sophisticated analyses so commonly and easily done with humans.

The two experiments reported here use earphones to extend previous work showing that budgerigars monitor the amplitude of their vocal output in the free-field (Manabe *et al.*, 1998). The use of earphones allows for the precise delivery and acoustic isolation of altered feedback and more closely matches the sophistication and refinement of work in humans. As in Manabe *et al.* (1998), both experiments required budgerigars to produce specific contact calls in response to a light cue, allowing us to know precisely what vocalization these animals would produce and when they would produce it.

In Experiment 1 (Lombard effect), we delivered amplitude-scaled white noise to subjects through the earphones while they were vocalizing. We tested these birds using a much broader range of noise levels than Manabe and colleagues (1998) and also examined whether, like humans, these birds show correlated changes in other acoustic parameters such as frequency and duration. Evidence of such changes would support the idea that both humans and budgerigars share similar mechanisms for maintaining intelligibility in noisy conditions. We hypothesized that: 1) vocal intensity would increase as the intensity of the auditory feedback increased, as reported previously in both budgerigars and humans, and, 2) there would be concomitant increases in both average vocal frequency and call duration, as described in the human literature. In Experiment 2 (Fletcher effect), we delivered amplitude-scaled templates of the birds' contact calls through the earphones that were temporally-aligned with their ongoing vocalizations. We hypothesized that: 1) vocal intensity would decrease as the intensity of the auditory feedback increased, and 2) there would be concomitant decreases in both average vocal frequency and call duration.

II. GENERAL METHODS

A. Subjects

The subjects in these experiments were three adult male budgerigars from a colony maintained in an aviary at the University of Maryland. Each bird was separately caged and had *ad libitum* access to water. Since food was used to reinforce vocal behavior, the birds were maintained at 90% of their free-feeding body weight.

The University of Maryland Animal Care and Use Committee approved all experimental procedures.

B. Apparatus

Birds were trained in an operant testing apparatus consisting of a small wire cage (14 cm x 12 cm x 17 cm) constructed of wire mesh and mounted in an acoustic isolation chamber (Industrial Acoustic Company model AC-1). Three light-emitting diodes (left, center, and right LEDs) were attached to a piece of anechoic foam on the front panel of the cage at approximately the level of the bird's head. Three small speakers (SONY model MDR-Q22LP) were mounted on the exterior of the cage – one at the center above the front LED panel and one on each of the left and right sides. A small directional microphone (SONY model ECM-77B), located just below the LED panel, detected vocalizations. A food hopper containing hulled millet was located on the floor of the cage under the front LED panel. A small video camera was used to monitor the bird's behavior while in the chamber. See Figure 3 for an image of this operant setup.

C. Training/Testing Procedure and Analysis

1. Contact Call Detection & Analysis

Training/testing and analysis programs were generated using MATLAB software and Tucker Davis Technologies (TDT) System III hardware (Gainesville, FL). The output of the microphone was amplified, low-pass filtered at 10 kHz, and sent to a circular memory buffer in a TDT real-time digital signal processor (RP2.1) at a nominal sampling rate of 25 kHz. A typical budgerigar contact call duration is 100-150 milliseconds with spectral energy concentrated between 2-4 kHz (Farabaugh and Dooling, 1996; Farabaugh *et al.*, 1998; Farabaugh *et al.*, 1994). Therefore, incoming signals were classified as a contact calls if signal intensity exceeded a user-defined value for a minimum of 70 milliseconds and if, during this time, the signal power in the frequency band between 2 and 4 kHz exceeded that measured between 4 and 10 kHz.

All signals classified as contact calls were sent to MATLAB and saved for later analysis. Analysis involved: 1) generation of power spectra iteratively across each call in 5 ms windows (with 50% window overlap), 2) measurement of several acoustic parameters from these power spectra, including average peak frequency, average peak amplitude, and 3 dB bandwidth of the spectral peak, and 3) calculation of whole-call measurements, including Wiener entropy (a unitless measure of disorder, see Tchernichovski *et al.*, 2001) and a similarity measure of the to-be-matched template call (see sections 3 and 4 below for a description of the template and correlation algorithm). These measures were analyzed using SPSS software. Also, peak frequency and peak amplitude contours, along with total power spectra, were saved for each call.

2. Initial Training (Shaping)

Birds were habituated to the experimental chamber and trained to eat from the food hopper when it was activated. Once the birds consistently ate from the raised hopper, manual shaping of vocalizations began. Here, typical aviary sounds were played in the operant chamber to induce the birds to vocalize. Whenever the birds responded to the aviary tape with a contact call, the experimenter activated the hopper. Birds quickly came to associate vocalizing in the test chamber with access to food and, therefore, tape playback was phased out over several training sessions.

When birds reliably produced contact calls in the absence of the aviary tape, vocal behavior was reinforced automatically.

Birds were next trained to vocalize only when the center LED was illuminated. Here, the LED turned off each time a vocalization was acquired and turned on again after a random time interval (approximately 5-15 seconds). Only vocalizations produced when the light was illuminated were reinforced. Vocalizations produced when the LED was turned off caused the random interval timer to reset and increased the wait time before the LED turned back on. Birds successfully completed this phase of training when they reliably vocalized in the chamber both without the flock tape and only in response to the illuminated center LED.

3. Contact Call Recognition

After completing the previous phase, birds were tested in several further training sessions to establish a call repertoire. The most typical contact call in a bird's repertoire was selected as that bird's "template" call (see Manabe and Dooling, 1997). A spectral cross-correlation program generated a similarity index between all calls produced in these sessions. This program created a spectrogram for each signal using a 256-point Hanning window with 50% window overlap. These spectrograms were then compared using a MATLAB 2-dimensional cross correlation algorithm (MATLAB function XCORR2). This algorithm generated a series of correlation values representing all possible temporal offsets between the two spectrograms. The maximum correlation value was taken as the similarity index between the two calls. This similarity index was then normalized so that it was zero if two calls were perfectly dissimilar and one if the calls were identical. A matrix of similarity values was constructed from all calls produced in a test session and was analyzed using a MALAB classical multidimensional scaling algorithm. The call in the center of the largest cluster in this two-dimensional space was selected as the template call for the next phase of training.

4. Template Training (Precision)

Subsequent training sessions used this template call in order to differentially reinforce vocal behavior. Birds were rewarded only for producing calls that were similar to the template call (using the same spectral cross-correlation algorithm described above). Every vocalization produced by a bird was compared to the stored digital template in real-time. The bird was reinforced if the correlation between the two calls exceeded a user-defined value. No reward was given if the correlation did not exceed this value. At first, the criterion correlation value was set very low (e.g., r = .01) so that all calls were reinforced. The criterion was gradually increased over several sessions to a maximum value of r = .70. All training sessions were terminated after 50 reinforcements or 25 minutes, whichever came first. Subjects were tested in two daily sessions, five days per week. All test sessions were separated by at least three hours.

D. Surgical Procedure and Earphone Construction

After all training procedures were completed, a small, stainless-steel headpost (jewelry pin w/ clutch back, Hirschberg Schutz & Co., Inc., Model #JC8425-01) was affixed to each bird’s skull. First, the animal was weighed and given an intramuscular injection of ketamine (40 mg/kg) / xylazine (20 mg/kg). The toe pinch response was used to determine whether the bird was properly anesthetized for surgery. Next, the superior aspect of the skull was exposed using a #11 scalpel blade and Vanass scissors (Fine Science Tools, Foster City, CA). The skull surface was abraded using the scalpel to create better adhesion before the headpost was attached using dental cement (A-M Systems Inc.). Nexaband was used to seal the incision, and the bird was placed in a heated therapy unit for monitoring until the anesthetic effects had worn off. Birds were monitored for 24-48 hours following surgery and a non-narcotic, non-steroidal analgesic (Flunixin meglumine, 10 mg/kg) was administered daily during this recovery period.

Following recovery, birds were fitted with earphones. The earphone frame was constructed using thin steel wire (1mm diameter) and small rubber grommets (10mm diameter). A transducer (Knowles Acoustics, Model #EH-3062) was glued to the interior of each grommet using commercially-available silicone sealant. When affixed to the headpost, the transducers were situated directly over the bird's ear canal openings and fitted as tightly to the bird's head as possible without causing obvious distress to the animal. All feedback stimuli were delivered to the bird through the earphones during a test session via small-diameter wiring from the TDT hardware through the ceiling of the operant chamber. The earphones could be easily attached to, or detached from, the headpost by fastening or unfastening the clutch back. Thus, birds were housed without the earphones attached - only the headpost was a permanent fixture on the birds' heads. The earphone apparatus was attached immediately prior to and was removed immediately following each session. See Figure 7 for an image of a budgerigar with earphones attached.

Figure 7. Image of a subject with a set of training earphones attached. Earphones were constructed of thin steel wire and rubber grommets and could easily be attached or removed from the animal. Refer to text for a complete description of earphone construction and attachment.

Following recovery from surgery, each bird was tested in several training sessions. This was necessary to ensure that performance was not obviously altered as a result of the surgery, wearing earphones, or the presence of wiring above the bird's head. No stimuli were delivered to the bird through the earphones during these sessions. All birds achieved and maintained a reinforcement rate greater than 90% within five sessions after being reintroduced into the testing environment following surgery.

III. EXPERIMENT 1: LOMBARD EFFECT

The Lombard effect describes an increase in vocal amplitude in response to an increase in ambient noise level. This phenomenon is well-studied in humans and has been shown in a number of nonhuman animals, including budgerigars. Here we sought to further examine the Lombard effect in budgerigars using a more rigorous methodology - including a broader range of noise levels and the use of earphones. We hypothesized that: 1) vocal intensity would increase as the intensity of the auditory feedback increased and, 2) there would be concomitant increases in both average vocal frequency and call duration, as described in the human literature.

B. Methods

1. Subjects

Three adult male budgerigars were used in this experiment.

D. Procedure

Once the birds were trained to asymptotic levels of performance on the template-training task described above and were fitted with earphones, a new testing phase was introduced in which Gaussian white noise was created using the TDT

System III RP2.1 hardware. This noise was delivered continuously through the earphones at varying intensity levels over the course of a session. The sound pressure level of the feedback was measured with a Larson-Davis Model 824 Sound Level Meter and 3-m extension cable with a ¼ in. microphone both before and after the experiment. The microphone was placed inside a custom-made adaptor which, when connected to the earphone transducer, allowed the experimenter to approximate the sound pressure level at the bird's ear when wearing the earphones. The sound pressure of the feedback was measured for 11 different noise levels (40 dB SPL to 90 dB SPL in 5 dB steps, A-weighting, fast RMS) at the bird's ear.

Birds were run in 4 sessions of 60 trials. Each session contained all 11 noise levels and a quiet condition (for a total of 12 feedback level conditions) randomly-presented in 5-trial blocks. All vocalizations produced during the experiment were stored digitally and analyzed off-line using a MATLAB signal analysis program. Analysis involved a two-step process in which calls were first sorted by noise level across sessions followed by an acoustic analysis of calls within each noise level. Acoustic measures included average peak frequency, average amplitude, and duration. Additionally, peak frequency and peak amplitude contours were generated for comparisons among the different noise levels.

C. Results and Discussion of Experiment 1

Figure 8 shows the mean call parameters for the three birds across noise levels as a series of scatterplots. These results show that budgerigars exhibit a robust Lombard effect while wearing earphones - mean intensity of all calls produced by the birds significantly increased by 7.8 dB SPL as the intensity of the noise feedback

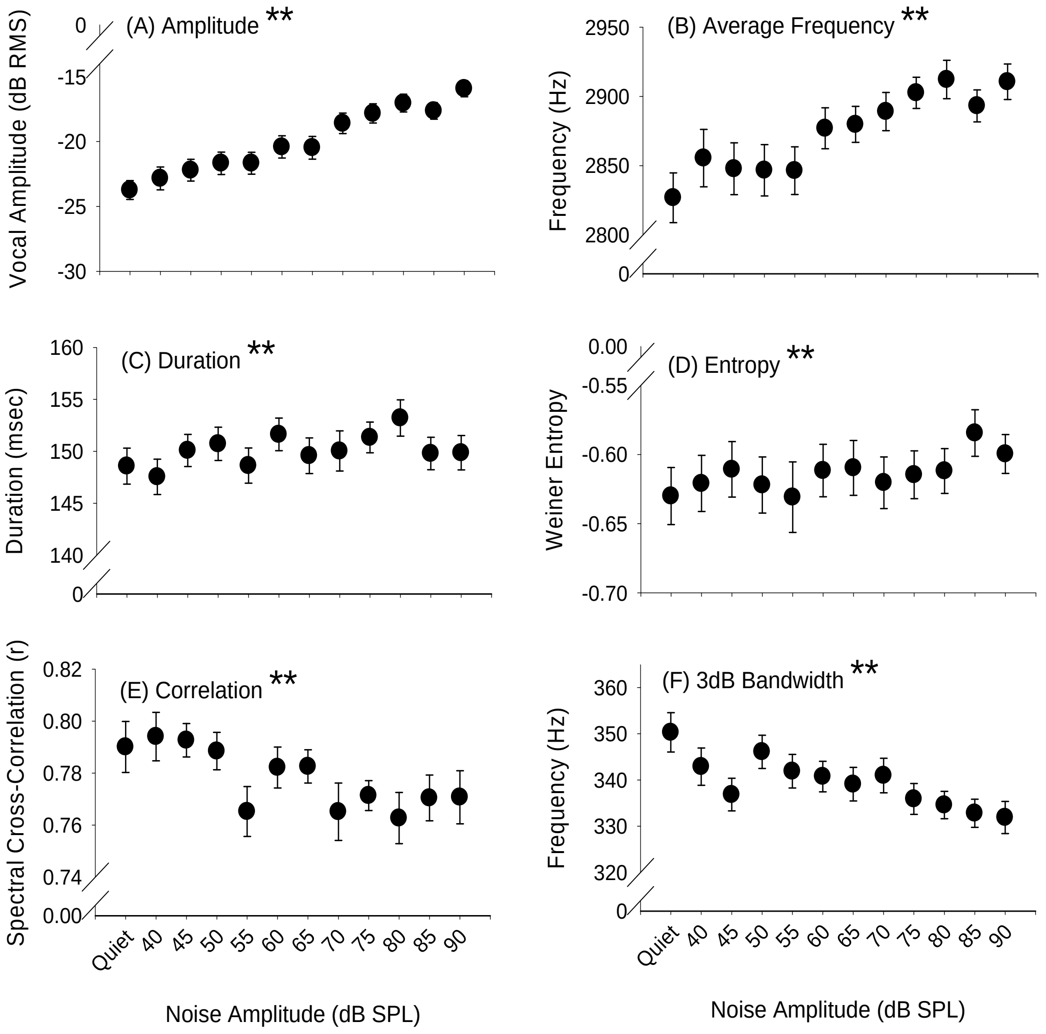

Figure 8. Mean and standard error of six acoustic measurements from calls produced under Lombard effect conditions. The largest changes were seen as increases in amplitude and average frequency. Smaller changes were seen in duration, entropy, similarity to template, and 3dB bandwidth. Double asterisks represent a significance level of < 0.01.

increased across a 50 dB range (Figure 8A) (One-way RM ANOVA; F[11,649] = 64.2, p < .01). Several other results parallel findings from work with humans. Average call frequency for the three birds significantly increased by 83.7 Hz across noise levels (Figure 8B) (One-way RM ANOVA; F[11,649] = 9.75, p < .01). These results show that, like humans, increases in vocal intensity in budgerigars are accompanied by related increases in call frequency. Mean call duration has a weak, but significant, positive relationship with noise level (Figure 8C) (One-way RM ANOVA; F[11,649] = 4.19, p < .01). These results suggest that budgerigars increase call length in response to increases in ambient noise in the way humans increase syllabic length when producing Lombard speech.

Wiener entropy showed a small, but significant, tendency toward zero as noise levels increased (Figure 8D) (One-way RM ANOVA; F[11,649] = 2.49, p < .01). A value of zero indicates pure white noise while increasing negative values indicate increasing tonality. This result indicates that the calls had become slightly more disordered as noise level increased. Both the similarity to call template and 3 dB bandwidth significantly decreased as noise levels increased (Figures 8E and 8F, respectively) (One-way RM ANOVA; F[11,649] = 2.42, p < .01, 3 dB bandwidth: One-way RM ANOVA; F[11,649] = 4.18, p < .01). The overall decrease in correlation values was slight (Δ r = .019), but indicates that vocalizations produced in noise exhibit small spectrotemporal changes in call structure. Changes in 3 dB bandwidth may reflect an attempt to counteract signal degradation in noisy conditions by narrowing the frequency range around the peak of the call spectrum.

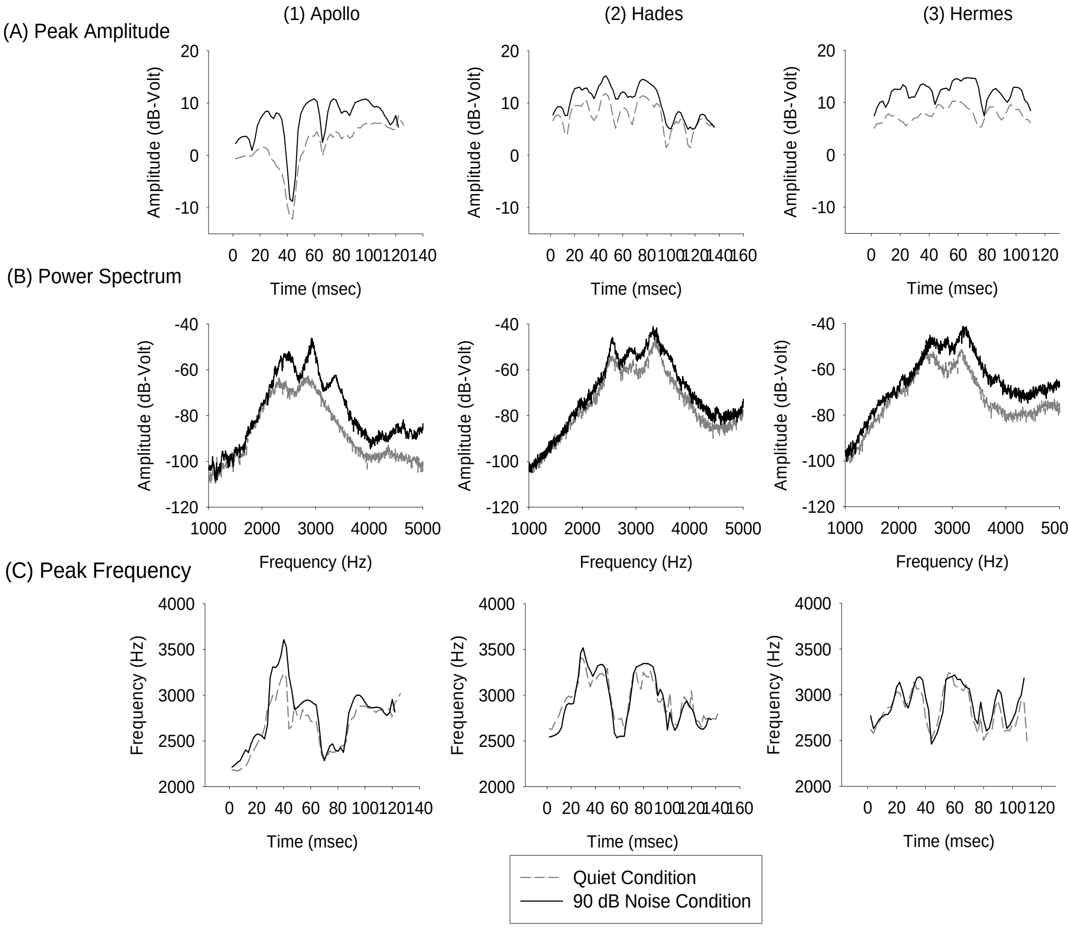

Figure 9. Amplitude contours, power spectra, and frequency contours from calls produced under Lombard effect conditions Overall, there was a significant increase in both amplitude and frequency which was shown as a raising of the contours from the 90 dB noise condition compared to contours from the quiet condition – these changes were also reflected in the power spectra. Changes in amplitude and frequency contours appear more pronounced in certain call segments compared to other segments.

Figure 9 shows changes in average peak amplitude (row A), power spectra (row B), and average peak frequency (row C) between calls produced in quiet and calls produced during presentation of 90 dB white noise. Average amplitude contours showed a general increase in vocal intensity between conditions. In one subject, this increase appears to occur only in the first half of the call (i.e., Panel A2). Similarly, the average frequency contours of all three birds show increases in vocal frequency, however certain call segments were altered far more then other segments (for example, Panel C1).

IV. EXPERIMENT 2: FLETCHER EFFECT

There were two important findings in the first experiment: 1) Budgerigars will vocalize for a food reward while wearing earphones, and 2) noise delivered through earphones elicits a robust Lombard effect in these animals. The first finding allows for other tests of auditory feedback. In particular, we can now test for the Fletcher effect in a nonhuman animal for the first time. As described before, the Fletcher effect is a decrease in vocal amplitude in response to an increase in perceived vocal loudness. In the following experiment, each bird’s stored template call was used as feedback and delivered through the earphones. The template call was chosen as the feedback stimulus instead of a bird’s own vocalization to ensure that the feedback was delivered at specific intensities and was not dependent on scaling a bird’s own vocal production (which itself was expected to vary in intensity during a session as the feedback volume was changed). The birds were trained to produce a specific call and informal analysis of the training sessions showed that those calls produced in an operant environment typically vary in duration by less than 5 milliseconds and amplitude by less than 3 dB. Therefore, we were confident that using the template as the feedback signal would be analogous to using feedback of the actual vocalization. We hypothesized that: 1) vocal intensity would decrease as the intensity of the auditory feedback increased and 2) there would be concomitant decreases in both average vocal frequency and call duration.

A. Method

1. Subjects

The three birds from Experiment 1 were used in this experiment.

B. Procedure

Each bird's call template used was used as the feedback stimulus. It was stored in a memory buffer in the TDT RP2.1 and delivered through the earphones at varying intensity levels. The RP2.1 immediately triggered playback of the amplitude-scaled call template through the earphones when a vocalization was detected at the microphone. There was a ~3 millisecond delay between onset of vocalization and playback through the earphones. This required that the feedback call be temporally-aligned with the bird's ongoing vocalization by removing the first 3 milliseconds of the template. As before, the SPL of the feedback was measured and calibrated as in Experiment 1 using a Larson-Davis Model 824 Sound Level Meter. The sound pressure of the feedback was measured for 3 different feedback levels (70, 80, and 90 dB SPL, A-weighting, fast RMS).

Birds were run in two sessions of 40 trials. Each session contained 8 amplitude levels (two each of 70 dB, 80 dB, 90 dB, and two no-feedback quiet conditions) randomly-presented in 5-trial blocks. These levels were chosen because informal analyses show that birds in the operant environment typically produce calls at ~70 dB SPL. As in Experiment 1, all vocalizations were stored digitally and analyzed off-line using a MATLAB signal analysis program. Analysis involved a two-step process in which calls were first sorted by noise level across sessions followed by an acoustic analysis of calls within each noise level. Acoustic measures included average peak frequency, average amplitude, and duration. Additionally, peak frequency and peak amplitude contours were generated for comparisons among the different noise levels.

C. Results and Discussion of Experiment 2

Figure 10 shows the mean call parameters for the three birds across noise levels as a series of scatterplots. Results show that budgerigars, like humans, exhibit a robust Fletcher effect while wearing earphones - mean intensity of all calls produced by the birds significantly decreased by 3.74 dB as the intensity of the call template feedback increased up to 90 dB (a roughly 25 dB SPL increase) (Figure 10A) (One-way RM ANOVA; F[3,177] = 38.5, $p < .01$). The Fletcher effect in budgerigars, as in humans, also results in concomitant decreases in call frequency - mean call frequency for the three birds across feedback levels significantly decreased by 59.1 Hz between the quiet condition and the 90 dB SPL feedback condition (Figure 10B) (One-way RM ANOVA; F[3,177] = 13.4, $p < .01$). Mean call duration had a significant, negative relationship with feedback level (Figures 10C) (One-way RM ANOVA; F[3,177] = 2.74, $p < .05$), suggesting that budgerigars decreased call length in response to increases in perceived vocal intensity.

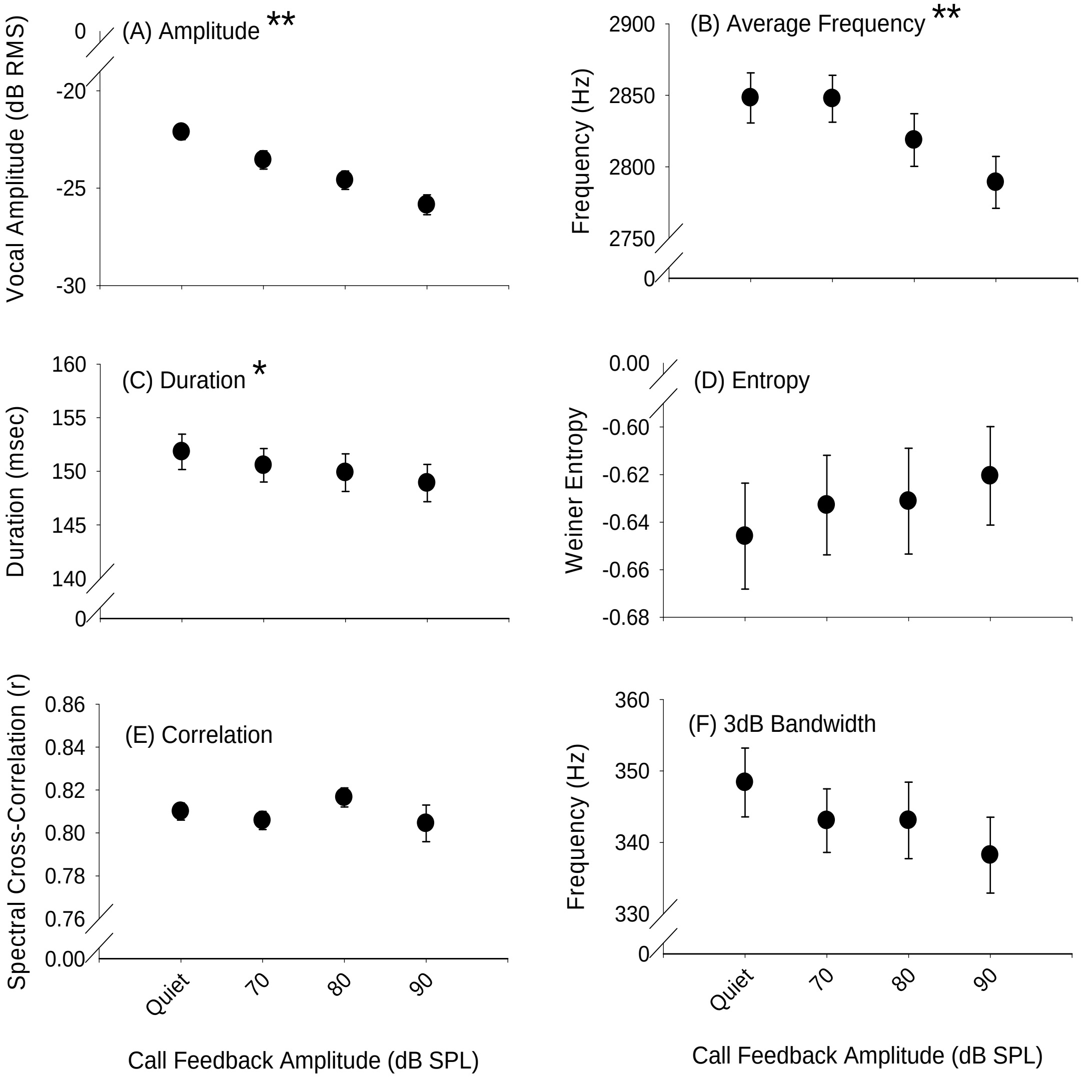

Figure 10. Mean and standard error of six acoustic measurements from calls produced under Fletcher effect conditions. The largest changes were seen as decreases in amplitude and average frequency, with smaller changes seen in duration. Double asterisks represent a significance level of < 0.01. Single asterisks represent significance level of < 0.05.

Wiener entropy showed a non-significant tendency toward zero as feedback levels increased (Figure 10D) (One-way RM ANOVA; F[3,177] = 1.19, p = .32). Neither similarity to call template nor 3 dB bandwidth significantly changed as feedback levels increased (Figures 10E and 10F, respectively) (Correlation: One-way RM ANOVA; F[3,177] = 1.14, p = .34, 3 dB bandwith: One-way RM ANOVA; F[3,177] = 1.99, p = .12). This suggests that the vocalizations did not exhibit obvious spectrotemporal changes in call structure. The non-significant trend toward decreased 3 dB bandwidth, seen both here and in Experiment 1, may reflect a general attempt to increase signal intelligibility or transmissibility in response to abnormal feedback conditions by narrowing the frequency range around the peak of the call spectrum.

Figure 11 shows changes in average peak amplitude (row A), power spectra (row B), and average peak frequency (row C) between calls produced in quiet and calls produced during presentation of 90 dB template call feedback. Average amplitude contours showed decreases in vocal intensity, although certain call segments were decreased more compared to other segments (e.g., Panel A2). The average frequency contours of all three birds show decreases in vocal frequency. Again, however, this change occurred primarily in specific call segments (for example, Panel C2). These results parallel findings from Experiment 1 showing that birds had made adjustments to particular call segments instead of changing the entire call.

We also looked at the calls produced on the first two trials in which call feedback was amplified in order to determine the time course of the Fletcher effect in budgerigars. Results showed no differences in amplitude across feedback levels when

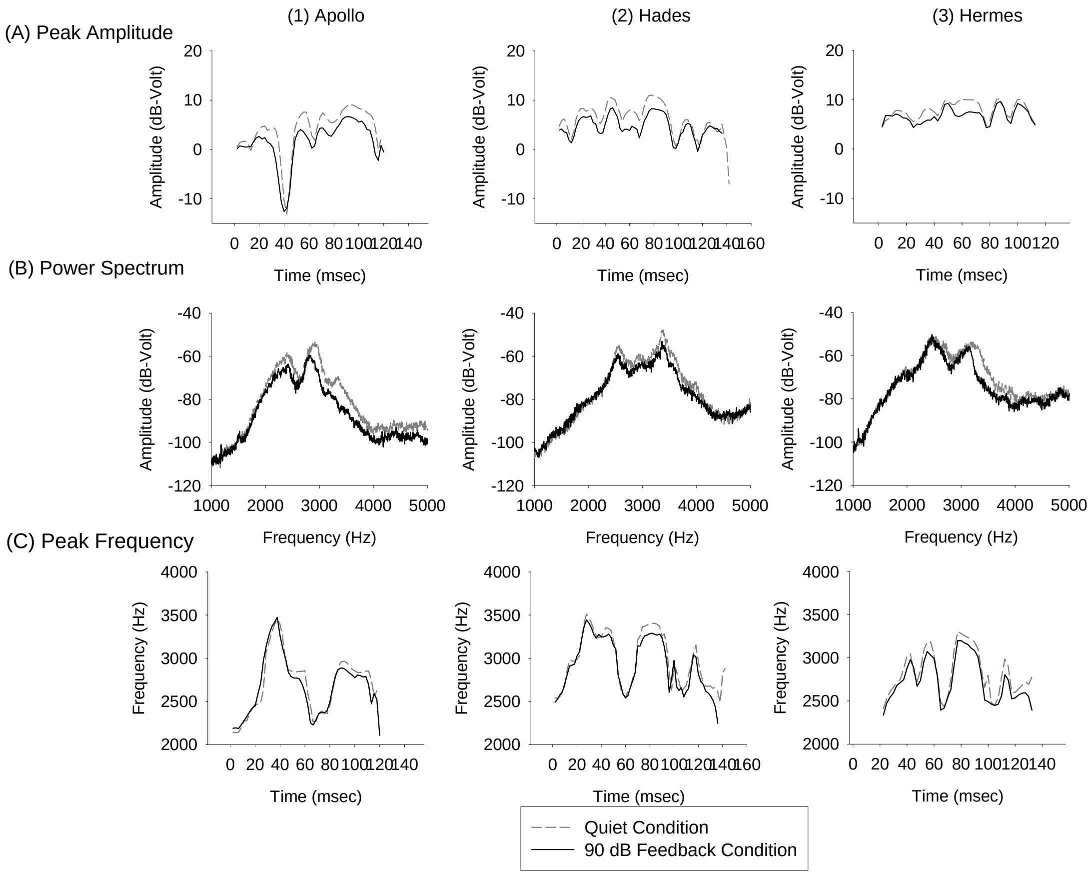

Figure 11. Amplitude contours, power spectra, and frequency contours from calls produced under Fletcher effect condtions. Overall, there was a significant decrease in both amplitude and frequency which was shown as a lowering of the contours from the 90 dB feedback condition compared to contours from the quiet condition – these changes were also reflected in the power spectra. Changes in amplitude and frequency contours are more pronounced in certain call segments compared to other segments.

comparing the first trial in which altered feedback was presented to the subjects (F[3,6] = 1.72, $p = 0.26$). There was also no difference in frequency across feedback levels (F[3,6] = 1.08, $p = 0.43$). However, the calls produced in the second feedback trial were significantly different across feedback levels in both amplitude (F[3,6] = 5.19, $p < 0.05$) and frequency (F[3,6] = 5.12, $p < 0.05$). These data show that budgerigars do not make immediate, online adjustments to the amplitude or frequency of their contact calls when provided with auditory feedback that is louder than normal during that same call. Instead, they make these adjustments in subsequent vocalizations. Consistent with this interpretation is that no changes were apparent in either the amplitude or frequency contours (based on visual comparison of the beginning and end of the contours) from the first feedback trial. Obvious changes toward the end of the contours would have suggested that these birds had adjusted their calls in real-time.

V. GENERAL DISCUSSION

Budgerigars depend on auditory feedback (AF) for normal vocal production. These birds show robust Lombard and Fletcher effects - increasing the intensity of their vocal output in the presence of background noise and decreasing the intensity of their vocal output when AF of their calls is artificially increased. This is a roughly linear relationship in which vocal amplitude is altered approximately 1 dB for every 5 dB change in AF amplitude. This is a somewhat shallower response slope compared to humans, where a 1 dB change in vocal amplitude occurs for each 2 to 3 dB change in AF amplitude (see Lane and Tranel, 1971). These intensity changes are associated with concomitant changes in contact call frequency and duration, a previously unreported finding in this species (e.g., Manabe *et al.*, 1998), but one that is consistent with descriptions of vocal effort in speech (e.g., Traunmüller and Eriksson, 2000). In humans, vocal effort is defined as the perceived work required for speaking. Increasing vocal effort results in increased amplitude, duration, and pitch while decreasing vocal effort show the opposite effects. Birds produce sound, like humans, through a set of vibrating structures in the sound producing organ (e.g., the syrinx in birds and the larnx in humans) which are driven by respiratory air flow (Fletcher and Tarnopolsky, 1999; Larsen and Goller, 1999, 2002). Budgerigars alter their vocal effort in a manner analogous to humans, which would be expected if increasing or decreasing vocal amplitude in this species is accomplished by increasing or decreasing, respectively, the velocity of the air passing through the syringeal membranes without changing membrane tension (e.g., Brittan-Powell *et al.*, 1997; Heaton *et al.*, 1995).

Budgerigars respond to these intensity changes by making adjustments to small call segments and not by modifying the entire call all at once. This piecemeal style of vocal modification occurred in both the amplitude and frequency structure of calls, although they appeared more obvious in the frequency domain. These results are consistent with previous work showing that calls are modified during vocal learning through changes in smaller acoustic segments rather than across the entire call (e.g., Farabaugh *et al.*, 1994; Manabe and Dooling, 1997). They also suggests the possibility of constraints on the plasticity of these calls in that certain call segments may be more amenable to change than others.

Budgerigars do not make these amplitude adjustments in real-time. Data from the Fletcher effect shows changes do not occur on the first trial containing amplitude-altered AF. Instead, effects occur on subsequent calls, presumably based on AF from the previous vocalization. Vocal amplitude adjustments based on altered feedback during sustained vowel production in humans occur in real-time within approximately 150-175 milliseconds of feedback onset (Bauer *et al.*, 2006; Heinks-Maldonado and Houde, 2005). This difference between humans and budgerigars may exist because contact calls are very short in duration (about 150 milliseconds) and compensatory changes in budgerigars may require a longer time frame. Hypothetically, then, a contact call significantly longer in duration than a normal call may show evidence of online amplitude adjustment. Alternatively, it is possible that contact calls in budgerigars are produced in a fashion more or less similar to songbird song syllables (Cynx, 1990; Franz and Goller, 2002; Riebel and Todt, 1997) and cannot be adjusted online regardless of call length. The operation of either mechanism would produce the results obtained in the current experiments.

Overall, though, we can assume that budgerigars actively assess the signal-to-noise ratio between their vocal behavior and their environment and make constant adjustments to their own vocal intensity in order to keep this ratio constant. We have measured changes in call frequency, duration, and 3dB bandwidth that are consistent with the idea that budgerigar vocal production contains a mechanism for overcoming the masking effects of environmental noise. Budgerigars form large, social flocks of loud and gregarious individuals and vocal production in such an environment would likely require a robust, fast-acting means of ensuring high signal-to-noise ratios during communicative exchanges. The present findings support the idea that such a mechanism exists in these birds.

Acknowledgments

We thank Elizabeth Brittan-Powell and Peter Marvit for comments on the manuscript. We also thank Leah Dickstein for help in performing the experiments. This work was supported by NIH grant DC-00198 to RJD, NIH grant DC-04664 to RJD, & NIH grant DC-006766 to MSO.

References

Bauer, J. J., Mittal, J., Larson, C. R., and Hain, T. C. (**2006**). "Vocal responses to unanticipated perturbations in voice loudness feedback: An automatic mechanism for stabilizing voice amplitude," Journal of the Acoustical Society of America 119, 2363-2371.

Boughman, J. W., and Moss, C. F. (**2003**). "Social sounds: Vocal learning and development of mammal and bird calls," in *Acoustic communication, springer handbook of auditory research*, edited by A. M. Simmons, A. N. Popper, and R. R. Fay (Springer-Verlag, New York), pp. 138-224.

Brittan-Powell, E. F., Dooling, R. J., Larsen, O. N., and Heaton, J. T. (**1997**). "Mechanisms of vocal production in budgerigars (melopsittacus undulatus)," The Journal Of The Acoustical Society Of America 101, 578-589.

Brumm, H., and Todt, D. (**2002**). "Noise-dependent song amplitude regulation in a territorial songbird.," Anim. Behav. 63, 891-897.

Cynx, J. (**1990**). "Experimental-determination of a unit of song production in the zebra finch (*taeniopygia guttata*)," J. Comp. Psychol. 104, 3-10.

Cynx, J., Lewis, R., Tavel, B., and Tse, H. (**1998**). "Amplitude regulation of vocalizations in noise by a songbird, taeniopygia guttata," Animal Behav. 56, 107-113.

Doupe, A. J., and Kuhl, P. K. (**1999**). "Birdsong and human speech: Common themes and mechanisms," Annu. Rev. Neurosci. 22, 567-631.

Draegert, G. L. (**1951**). "Relationships between voice variables and speech intelligibility in high level noise," Speech Monographs 18, 272-278.

Dreher, J. J., and O'Neill, J. J. (**1958**). "Effects of ambient noise on speaker intelligibility of words and phrases," Laryngoscope 68, 539-548.

Farabaugh, S., and Dooling, R. J. (**1996**). "Acoustic communication in parrots: Laboratory and field studies of budgerigars, *melopsittacus undulatus*," in *Ecology and evolution of acoustic communication in birds*, edited by D. E. Kroodsma, and E. H. Miller (Cornell University Press, Ithaca, NY), pp. 97-118.

Farabaugh, S. M., Dent, M. L., and Dooling, R. J. (**1998**). "Hearing and vocalizations in native australian budgerigars (melopsittacus undulatus)," J. Comp. Psychol. 112, 74-81.

Farabaugh, S. M., Linzenbold, A., and Dooling, R. J. (**1994**). "Vocal plasticity in budgerigars (*melopsittacus undulatus*): Evidence for social factors in the learning of contact calls," J. Comp. Psychol. 108, 81-92.

Fletcher, N. H., and Tarnopolsky, A. (**1999**). "Acoustics of the avian vocal tract," Journal of the Acoustical Society of America 105, 35-49.

Franz, M., and Goller, F. (**2002**). "Respiratory units of motor production and song imitation in the zebra finch," J Neurobiol 51, 129-141.

Hanley, T. D., and Steer, M. D. (**1949**). "Effect of level of distracting noise upon speaking rate, duration and intensity," Journal of Speech & Hearing Disorders 14, 363-368.

Heaton, J. T., Farabaugh, S. M., and Brauth, S. E. (**1995**). "Effect of syringeal denervation in the budgerigar (melopsittacus undulatus): The role of the syrinx in call production," Neurobiology of Learning and Memory 64, 68-82.

Heinks-Maldonado, T. H., and Houde, J. F. (**2005**). "Compensatory responses to brief perturbations of speech amplitude," Acoustics Research Letters Online 6, 131-137.

Janik, V. M., and Slater, P. J. B. (**1997**). "Vocal learning in mammals," in *Advances in the study of behaviour*, edited by P. J. B. Slater, J. S. Rosenblatt, C. T. Snowdon, and H. Milinski (Academic Press, New York), pp. 59-99.

Janik, V. M., and Slater, P. J. B. (**2000**). "The different roles of social learning in vocal communication," Animal Behavior 60, 1-11.

Kobayashi, K. I., and Okanoya, K. (**2003**). "Context-dependent song amplitude control in bengalese finches," Neuroreport 14, 521-524.

Lane, H., and Tranel, B. (**1971**). "Lombard sign and role of hearing in speech," Journal of Speech and Hearing Research 14, 677-709.

Larsen, O. N., and Goller, F. (**1999**). "Role of syringeal vibrations in bird vocalizations," P Roy Soc Lond B Bio 266, 1609-1615.

Larsen, O. N., and Goller, F. (**2002**). "Direct observation of syringeal muscle functions in songbirds and a parrot," J Exp Biol 205, 25-35.

Lombard, E. (**1911**). "Le signe de l'élévation de la voix," Ann. Maladies Oreille, Larynx, Nez, Pharynx 37, 101-119.

Manabe, K., and Dooling, R. J. (**1997**). "Control of vocal production in budgerigars (melopsittacus undulatus): Selective reinforcement, call differentiation, and stimulus control," Behav Process 41, 117-132.

Manabe, K., Sadr, E. I., and Dooling, R. J. (**1998**). "Control of vocal intensity in budgerigars (*melopsittacus undulatus*): Differential reinforcement of vocal intensity and the lombard effect," J. Acoust. Soc. Am. 103, 1190-1198.

Potash, L. M. (**1972**). "Noice-induced changes in calls of the japanese quail.," Psychon. Sci. 26, 252-254.

Pytte, C. L., Rusch, K. M., and Ficken, M. S. (**2003**). "Regulation of vocal amplitude by the blue-throated hummingbird, *lampornis clemenciae*," Animal Behaviour 66, 703-710.

Riebel, K., and Todt, D. (**1997**). "Light flash stimulation alters the nightingale's singing style: Implications for song control mechanisms," Behaviour 134, 789-808.

Siegel, G. M., and Pick, H. L. (**1974**). "Auditory feedback in the regulation of voice," Journal of the Acoustical Society of America 56, 1618-1624.

Sinnott, J. M., Stebbins, W. C., and Moody, D. B. (**1975**). "Regulation of voice amplitude by the monkey," J. Acoust. Soc. Am. 58, 412-414.

Tchernichovski, O., Mitra, P. P., Lints, T., and Nottebohm, F. (**2001**). "Dynamics of the vocal imitation process: How a zebra finch learns its song," Science 291, 2564-2569.

Traunmüller, H., and Eriksson, E. (**2000**). "Acoustic effects of variation in vocal effort by men, women, and children," Journal of the Acoustical Society of America 107, 3438-3451.

Chapter 4 - Internal Control: II. Spectrotemporally Misaligned Auditory Feedback.

I. INTRODUCTION

It is well established that spectrotemporally-correct auditory feedback (AF) is important for the normal development and maintenance of vocal production in humans. One of the oldest investigations of these phenomena has focused on the effect of delayed auditory feedback (DAF) on human speech (e.g., Lee, 1950; for a review, see Yates, 1963). Delaying the speech signal causes a spectrotemporal mismatch between the expected and actual AF and results in a number of disruptive effects, including slower speech rate, higher fundamental frequency, longer syllable durations, and a range of production errors (including stuttering and short consonant-like bursts of sound; some subjects report a complete inability to continue speaking (Fairbanks, 1955; Howell and Archer, 1984; Lee, 1950; Yates, 1963). The most severe disruptions occur at a delay length of about 200 milliseconds, with decreasing impairment at shorter and longer delays. Another well-documented consequence of DAF is its fluency-enhancing effects on stutterers (e.g., Bloodstein, 1995). Overall, this suite of effects has been interpreted as evidence for timing malfunctions in a closed-loop feedback circuit which controls ongoing vocal production via auditory feedback (e.g., Chase, 1965; Fairbanks, 1954).

There is great interest in uncovering the mechanisms that give rise to the DAF effect in humans. Such knowledge may benefit individuals with speech dysfluencies, inform models of speech production, provide insight into mechanisms of language learning, and, more generally, contribute to an overall better understanding of how closed-loop serial behavior is performed (Bloodstein, 1995; Chase, 1965; Fairbanks, 1954, 1955; Finney and Warren, 2002; Yates, 1963). Unfortunately, studies of the DAF effect have been limited by the fact that invasive physiological and anatomical work is impossible to perform in humans. Therefore, tests of DAF have been restricted to behavioral work and model-building. An animal system would provide opportunities to test DAF models and examine neural mechanisms using procedures impossible to perform in humans.

Birds undoubtedly represent the best animal model for studies of vocal learning and the role of AF in vocal production (e.g., Brainard and Doupe, 2000; Doupe and Kuhl, 1999; Konishi, 2004). Recent work in songbirds has examined the effects of perturbing AF by playing spectrotemporally altered song during vocal production (Cynx and Von Rad, 2001; Leonardo and Konishi, 1999; Sakata and Brainard, 2006). These studies report dramatic decreases in a bird's ability to produce normal song when presented with spectrotemporally-altered auditory feedback. Specifically, birds show song syllable repetition, syllable deletion, and loss of syllable sequencing and structure under these conditions. The most severe disruptions occur at delays of 100 milliseconds in zebra finches (Cynx and Von Rad, 2001) and about 65 milliseconds in Bengalese finches (Sakata and Brainard, 2006).

Parrots (Psittaciformes) are the second largest order of birds that exhibit vocal learning and this ability is believed to have evolved independently of the songbird order (e.g., Farabaugh and Dooling, 1996; Kroodsma and Miller, 1982; Nottebohm, 1972; Striedter, 1994). Of the various parrot species examined, budgerigars are the most well-studied in terms of their auditory capabilities, vocal behavior, and vocal learning (see review in Farabaugh and Dooling, 1996) and may be more analogous to the human system than songbirds in several ways. For example, vocal learning in budgerigars requires a normally functioning auditory system, occurs over the course of only a few days, has been reported in both males and females, and is independent of age and season (e.g., Brittan-Powell *et al.*, 1997; Farabaugh and Dooling, 1996; Farabaugh *et al.*, 1994; Hile *et al.*, 2000; Hile and Striedter, 2000; Striedter, 1994). Such learning has been shown to occur during a change in social settings (Brown *et al.*, 1988; Farabaugh *et al.*, 1994; Hile *et al.*, 2000; Hile and Striedter, 2000; Striedter *et al.*, 2003). Unlike most songbirds, the budgerigar vocal communication system, which includes contact calls and a long, rambling, non-stereotyped warble song (Brockway, 1964a, b; 1969; Farabaugh *et al.*, 1992), remains highly plastic throughout adulthood.

The two experiments reported here represent the first test of spectrotemporal alterations of AF in budgerigars. Subjects were trained to produce contact calls while AF stimuli were delivered through earphones mounted on the birds' heads, which more closely matches the sophistication and refinement of work in humans. Experiment 1 looked at the effect of DAF of the bird's own vocalizations on vocal production. We hypothesized that, as in the human and songbird literature, vocalizations produced under DAF conditions would be disrupted relative to those produced under non-DAF conditions. We expected such disruptions to involve vocalizations with a non-typical acoustic structure (e.g., changes in pitch, duration, or spectrotemporal structure relative to contact calls the birds were trained to produce).

Experiment 2 looked at the effect of grossly altering the spectrotemporal structure of AF. We did this by presenting either a temporally-reversed version of the birds' template call or a different bird's call as feedback stimuli. The first manipulation preserved the spectral content of the AF while changing the temporal structure; the second manipulation altered both the spectral and temporal characteristics of the AF. To the best of our knowledge, these kinds of manipulations have not been done in either humans or songbirds. We hypothesized that, as in Experiment 1, vocalizations produced under both of these altered AF conditions would be disrupted compared to non-altered AF conditions and that these disruptions would involve an abnormal acoustic structure.

II. GENERAL METHODS

A. Subjects

The subjects in this experiment were three adult budgerigars from a colony maintained in an aviary at the University of Maryland. Each bird was separately caged and had *ad libitum* access to water. Since food was used to reinforce vocal behavior, the birds were maintained at 90% of their free-feeding body weight. The University of Maryland Animal Care and Use Committee approved all experimental procedures.

B. Apparatus

Birds were trained in an operant testing apparatus consisting of a small wire cage (14 cm x 12 cm x 17 cm) constructed of wire mesh and mounted in an acoustic isolation chamber (Industrial Acoustic Company model AC-1). Three light-emitting diodes (left, center, and right LEDs) were attached to a piece of anechoic foam on the front panel of the cage at approximately the level of the bird's head. Three small speakers (SONY model MDR-Q22LP) were mounted on the exterior of the cage – one at the center above the front LED panel and one on each of the left and right sides. A small directional microphone (SONY model ECM-77B), located just below the LED panel, detected vocalizations. A food hopper containing hulled millet was located on the floor of the cage under the front LED panel. A small video camera was used to monitor the bird's behavior while in the chamber. See Figure 3 for an image of this operant setup.

C. Training/Testing Procedure and Analysis

1. Contact Call Detection & Analysis

Training/testing and analysis programs were generated using MATLAB software and Tucker Davis Technologies (TDT) System III hardware (Gainesville, FL). The output of the microphone was amplified, low-pass filtered at 10 kHz, and sent to a circular memory buffer in a TDT real-time digital signal processor (RP2.1) at a nominal sampling rate of 25 kHz. A typical budgerigar contact call has a duration of 100-150 milliseconds and spectral energy concentrated between 2-4 kHz (Farabaugh and Dooling, 1996; Farabaugh *et al.*, 1998; Farabaugh *et al.*, 1994). Therefore, incoming signals were classified as a contact calls if signal intensity exceeded a user-defined value for a minimum of 70 milliseconds and if, during this time, the signal power in the frequency band between 2 and 4 kHz exceeded that measured between 4 and 10 kHz.

All signals classified as contact calls were sent to MATLAB and saved for later analysis. Analysis involved: 1) generation of power spectra iteratively across each call in 5 ms windows (with 50% window overlap), 2) measurement of several acoustic parameters from these power spectra, including average peak frequency, average peak amplitude, and 3 dB bandwidth of the spectral peak, and 3) calculation of whole-call measurements, including duration, Wiener entropy (a unitless measure of disorder, see Tchernichovski *et al.*, 2001) and a similarity measure of the to-be-matched template call (see sections 3 and 4 below for a description of the template and correlation algorithm). These measures were analyzed using SPSS software. Also, peak frequency contours were saved for each call.

2. Initial Training (Shaping)

Birds were habituated to the experimental chamber and trained to eat from the food hopper when it was activated. Once the birds consistently ate from the raised hopper, manual shaping of vocalizations began. Here, typical aviary sounds were played in the operant chamber to induce the birds to vocalize. Whenever the birds responded to the aviary tape with a contact call, the experimenter activated the hopper. Birds quickly came to associate vocalizing in the test chamber with access to food and, therefore, tape playback was phased out over several training sessions. When birds reliably produced contact calls in the absence of the aviary tape, vocal behavior was reinforced automatically.

Birds were next trained to vocalize only when the center LED was illuminated. Here, the LED turned off each time a vocalization was acquired and turned on again after a random time interval (approximately 5-15 seconds). Only vocalizations produced when the light was illuminated were reinforced. Vocalizations produced when the LED was turned off caused the random interval timer to reset and increased the wait time before the LED turned back on. Birds successfully completed this phase of training when they reliably vocalized in the chamber both without the flock tape and only in response to the illuminated center LED.

3. Contact Call Recognition

After completing the previous phase, birds were tested in several further training sessions so that a call repertoire could be established. The most typical contact call in a bird's repertoire was selected as that bird's "template" call (Manabe and Dooling, 1997). A spectral cross-correlation program generated a similarity index between all calls produced in these sessions. This program created a spectrogram for each signal using a 256-point Hanning window with 50% window overlap. These spectrograms were then compared using a MATLAB 2-dimensional cross correlation algorithm (MATLAB function XCORR2). This algorithm generated a series of correlation values representing all possible temporal offsets between the two spectrograms. The maximum correlation value was taken as the similarity index between the two calls. This similarity index was then normalized so that it was zero if two calls were perfectly dissimilar and one if the calls were identical. A matrix of similarity values was constructed from all calls produced in a test session and was analyzed using a MALAB classical multidimensional scaling algorithm. The call in the center of the largest cluster in this two-dimensional space was selected as the template call for the next phase of training.

4. Template Training (Precision)

Subsequent training sessions used this template call in order to differentially reinforce vocal behavior. Birds were rewarded only for producing calls that were similar to the template call. This was accomplished by using the same spectral cross-correlation algorithm described above. Every vocalization produced by a bird was compared to the stored digital template in real-time. The bird was reinforced if the correlation between the two calls exceeded a user-defined value. No reward was given if the correlation did not exceed this value. At first, the criterion correlation value was set very low (e.g., r = .01) so that all calls were reinforced. The criterion was gradually increased over several sessions to a maximum value of r = .70. All training sessions were terminated after 50 reinforcements or 25 minutes, whichever came first. Subjects were tested in two daily sessions, five days per week. All test sessions were separated by at least three hours.

D. Surgical Procedure and Earphone Construction

After all training procedures were completed, a small, stainless-steel headpost (jewelry pin w/ clutch back, Hirschberg Schutz & Co., Inc., Model #JC8425-01) was affixed to each bird's skull. First, the animal was weighed and given an intramuscular injection of ketamine (40 mg/kg) / xylazine (20 mg/kg). The toe pinch response was used to determine whether the bird was properly anesthetized for surgery. Next, the superior aspect of the skull was exposed using a #11 scalpel blade and Vanass scissors (Fine Science Tools, Foster City, CA). The skull surface was abraded using the scalpel to create better adhesion before the headpost was attached using dental cement (A-M Systems Inc.). Nexaband was used to seal the incision, and the bird was placed in a heated therapy unit for monitoring until the anesthetic effects had worn off. Birds were monitored for 24-48 hours following surgery and a non-narcotic, non-steroidal analgesic (Flunixin meglumine, 10 mg/kg) was administered daily during this recovery period.

Following recovery, birds were fitted with earphones. The earphone frame was constructed using thin steel wire (1mm diameter) and small rubber grommets (10mm diameter). A transducer (Knowles Acoustics, Model #EH-3062) was glued to the interior of each grommet using commercially-available silicone sealant. When affixed to the headpost, the transducers were situated directly over the bird's ear canal openings and fitted as tightly to the bird's head as possible without causing obvious distress to the animal. All feedback stimuli were delivered to the bird through the earphones during a test session via small-diameter wiring from the TDT hardware through the ceiling of the operant chamber. The earphones could be easily attached to, or detached from, the headpost by fastening or unfastening the clutch back. Thus, birds were housed without the earphones attached - only the headpost was a permanent fixture on the birds' heads. The earphone apparatus was attached immediately prior to and was removed immediately following each session. See Figure 7 for an image of a budgerigar with earphones attached.

Following recovery from surgery, each bird was tested in several training sessions. This was necessary to ensure that performance was not obviously altered as a result of the surgery, wearing earphones, or the presence of wiring above the bird's head. No stimuli were delivered to the bird through the earphones during these sessions. All birds achieved and maintained a reinforcement rate greater than 90% within five sessions after being reintroduced into the testing environment following surgery.

III. EXPERIMENT 1: DELAYED AUDITORY FEEDBACK

C. Methods

1. Subjects

Three adult male budgerigars were used in this experiment.

E. Procedure

Once the birds were trained to asymptotic levels of performance on the template-training task described above and were fitted with earphones, a new testing phase was introduced in which the RP2.1 immediately triggered playback of the incoming microphone signal through the earphones whenever a vocalization was detected at the microphone. This signal was delivered as AF with a user-specified time delay to examine whether these birds show a DAF response.

Delay lengths ranged from 0 ms to 100 ms in 25 ms increments. A minimum delay of 25 milliseconds was chosen because studies of the precedence effect show that budgerigars perceptually suppress correlated sounds that occur within 20 milliseconds of each other (e.g., Dent and Dooling, 2003a, 2003b, 2004) and we wanted to avoid this condition. The TDT RP2.1 processing chain (A/D conversion → digital delay of the incoming signal → D/A conversion) put an additional 3 millisecond delay on the signal path. Therefore, feedback in the 0 ms delay condition was actually delayed by approximately 3 milliseconds. The average duration of contact calls produced by the birds in this experiment was 152 +/- 6.2 milliseconds. Feedback, then, would begin after about 1.9% (in the 0 ms delay condition) to about 65.8% (in the 100 ms delay condition) of the bird's vocalization had already been produced, depending on the specific subject.

The sound pressure level of the feedback was set as close to 70 dB SPL at each bird's ear as possible, as measured by a Larson-Davis Model 824 Sound Level

Meter and 3-m extension cable with a ¼ in. microphone both before and after the experiment. The microphone was placed inside a custom-made adaptor which, when connected to the earphone transducer, allowed the experimenter to approximate the sound pressure level at the bird's ear when wearing the earphones. A level of 70 dB was chosen because this is the approximate level of vocalizations produced by birds in the experimental chamber.

Birds were run in two sessions per delay length. Only one delay length was used per session. Each session was comprised of 70 trials: 10 feedback trials and 60 non-feedback (quiet) trials. Feedback trials were randomized across a session such that one feedback trial was presented approximately every 3-8 trials. All vocalizations were stored digitally and analyzed off-line using a MATLAB signal analysis program. Analysis involved a two-step process in which calls were first sorted by trial type (i.e., pre-feedback trials, feedback trials, first trial post-feedback, second trial post-feedback, and all other trials). Step two involved an acoustic analysis of calls within each trial type. Acoustic measures included peak frequency, amplitude, duration, and similarity to template. Additionally, peak frequency contours were generated to facilitate comparisons among the different trial types.

Contact calls were classified as "errors" based on one or more of the following criteria: 1) a correlation (similarity to template) value below 60%, 2) an average frequency differing by more than 250 Hz from the average frequency of a subject's trained call, and/or 3) a duration that was 20% longer or shorter than the average duration of a subject's trained call. In a typical training session for these subjects, the average similarity score was higher than 70%, the average frequency varied by < 100 Hz, and the duration varied by < 7%. Errors, as defined here, are typically rare occurrences.

D. Results and Discussion of Experiment 1

All three birds showed severe disruptions in several vocalizations produced under conditions of delayed auditory feedback. There were 60 DAF trials per delay length (20 per subject) and a total of 53 errors were produced as a result (the three individual birds produced 18, 22, and 13 errors). Calls were classified as errors based on correlation and duration differences. No calls were flagged as errors based solely on peak frequency values. In other words, no calls differed by more than 250 Hz without concomitant changes in either correlation or duration.

Errors generally fell into three categories (see Table 3, left column for comparisons between errors and trained calls for each acoustic measure): The first was the same call-type, but with acoustic elements added or subtracted. This type of error represented 28.3% of all errors and, across all three birds, was associated with a significantly lower correlation value compared to the trained calls; no other acoustic measures were significantly different across all subjects (Table 3). Inclusion in this category was based on differences in duration between errors and trained contact calls, but overall duration was not significantly different because two subjects produced errors which were longer than trained calls (191.9 and 204.9 ms to 145.4 and 168.6 ms, respectively) while the third subject produced errors which were shorter than the trained calls (110.3 ms to 145.7 ms, respectively). Second, a different call-type was produced. These were the most frequent errors (62.3% of all errors) and vocalizations in this category had a significantly lower correlation, peak frequency,

Table 3. Differences in Acoustic Measures Between Error Calls and Trained Calls

	DAF		Reversed/Other	
Acoustic Measures	**t(2)**	**Significance**	**t(2)**	**Significance**
Error I				
Correlation	**4.32**	**0.05**	1.88	0.20
Average Frequency	-0.08	0.94	0.19	0.87
3 dB Bandwidth	-1.79	0.22	3.39	0.08
Amplitude	1.09	0.39	0.32	0.78
Duration	-0.62	0.60	-0.08	0.94
Wiener Entropy	0.78	0.52	**-5.79**	**< 0.05**
Error II				
Correlation	**16.2**	**< 0.01**	**7.80**	**< 0.05**
Average Frequency	**5.28**	**< 0.05**	**5.47**	**< 0.05**
3 dB Bandwidth	**4.83**	**< 0.05**	**6.27**	**< 0.05**
Amplitude	**5.37**	**< 0.05**	4.03	0.57
Duration	2.13	0.17	0.45	0.69
Wiener Entropy	-1.11	0.38	-0.28	0.81
Error III				
Correlation	**5.65**	**< 0.05**	N/A	
Average Frequency	0.38	0.74		
3 dB Bandwidth	0.25	0.83		
Amplitude	**8.52**	**< 0.05**		
Duration	**6.56**	**< 0.05**		
Wiener Entropy	-1.05	0.40		

Measures in **BOLD** are significantly different between error and trained calls and amplitude and a narrower 3dB bandwidth across all subjects compared to trained contact calls (see Table 3). Third, shorter acoustic elements that did not resemble a complete contact call were produced. These were the least frequent (9.4% of all errors), but the most obviously abnormal, of all errors. These vocalizations had a significantly lower correlation, amplitude, and duration compared to a subject's trained calls (Table 3). Examples from each of these categories are shown as spectrograms in Figure 12 along with the relevant template call that each subject was trained to match.

Error rates differed as a function of delay length. As in humans, there was a maximally-disruptive delay under which DAF produced the most errors in budgerigar calls (i.e., 49.6% of all errors occurred at a delay of 25 ms). Longer delay lengths resulted in comparatively fewer errors (One-way RM ANOVA; F[4,8] = 24.01, $p < .001$). The majority (i.e., 83.0%) of errors occurred within the first two calls after a feedback trial and, of those errors, most (77.3%) occurred on the first call following feedback. No errors occurred on the feedback trial itself. Looking only within the first two calls after a feedback trial, error rates were highest in the 25 millisecond delay condition (i.e., an error was produced within the first two calls following a DAF trial 41.7% of the time) compared to longer delay lengths (Figure 13, left panel). There was no difference in the error rate between the first and last half of a session (Paired samples t-test; t[2] = 1.39, $p = 0.30$), showing that error rate did not increase or decrease as a result of experience with DAF.

Figure 14 shows changes in the average frequency contours of contact calls across trial types (i.e., pre-feedback trials [Pre], feedback trials [AF], first trial post-

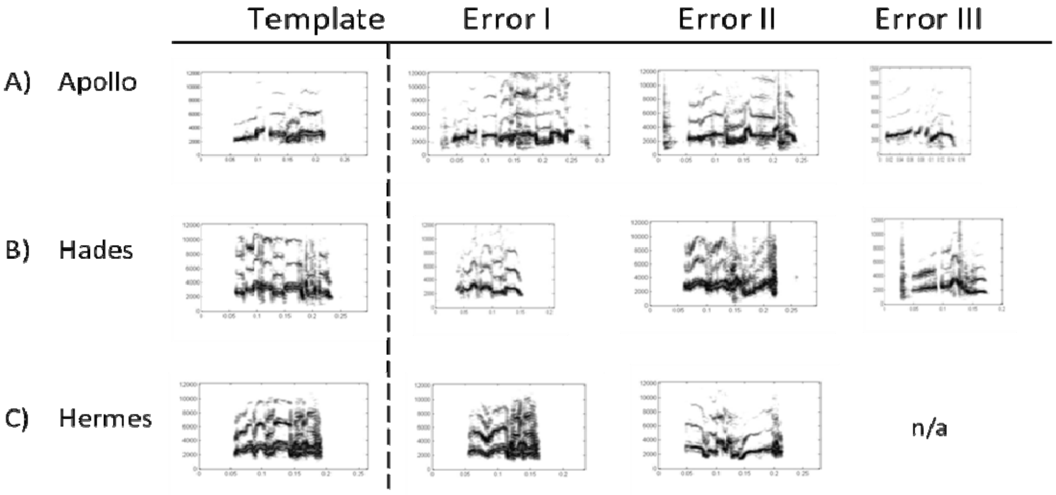

Figure 12. Spectrograms showing the template call and examples of errors produced under conditions of delayed auditory feedback. The first kind of error (Error I) was produced when a subject added or subtracted call elements from its trained call. The second kind of error (Error II) occurred when the vocalization did not match the template ($r < 0.60$), but was still recognizable as a complete contact call. A third kind (Error III) were those that did not match the template and did not resemble a complete contact call.

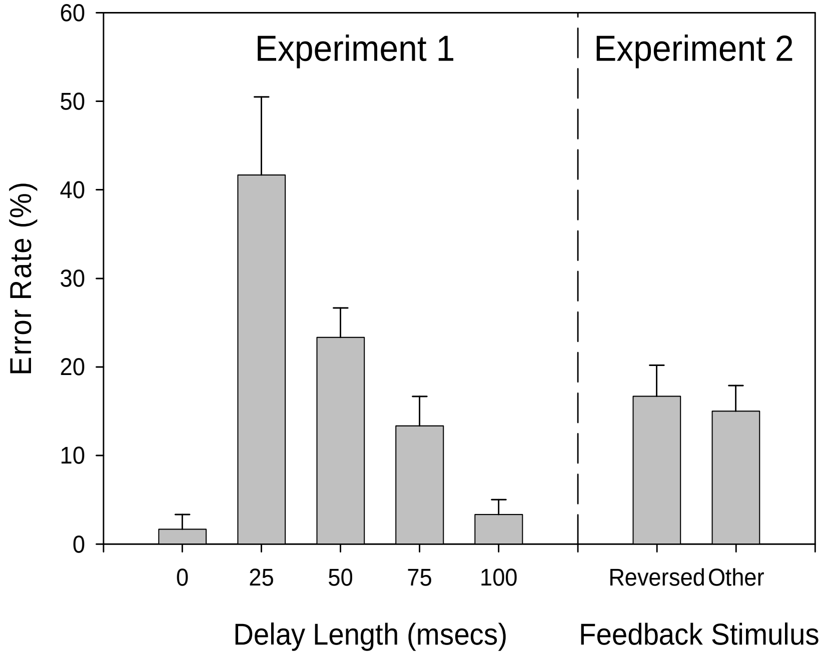

Figure 13. **Error rate varies as a function of feedback delay length (Experiment 1) and feedback type (Experiment 2). Mean and standard error for each of the five delay lengths shows that birds produced errors within the first two calls after feedback 41.7% of the time in those sessions with feedback delays of 25 ms. Comparatively fewer errors were produced as delay length increased. Similarly, errors were produced within the first two calls after either 'reversed call' or 'other call' feedback on 16.7% and 15.0% of trials, respectively.**

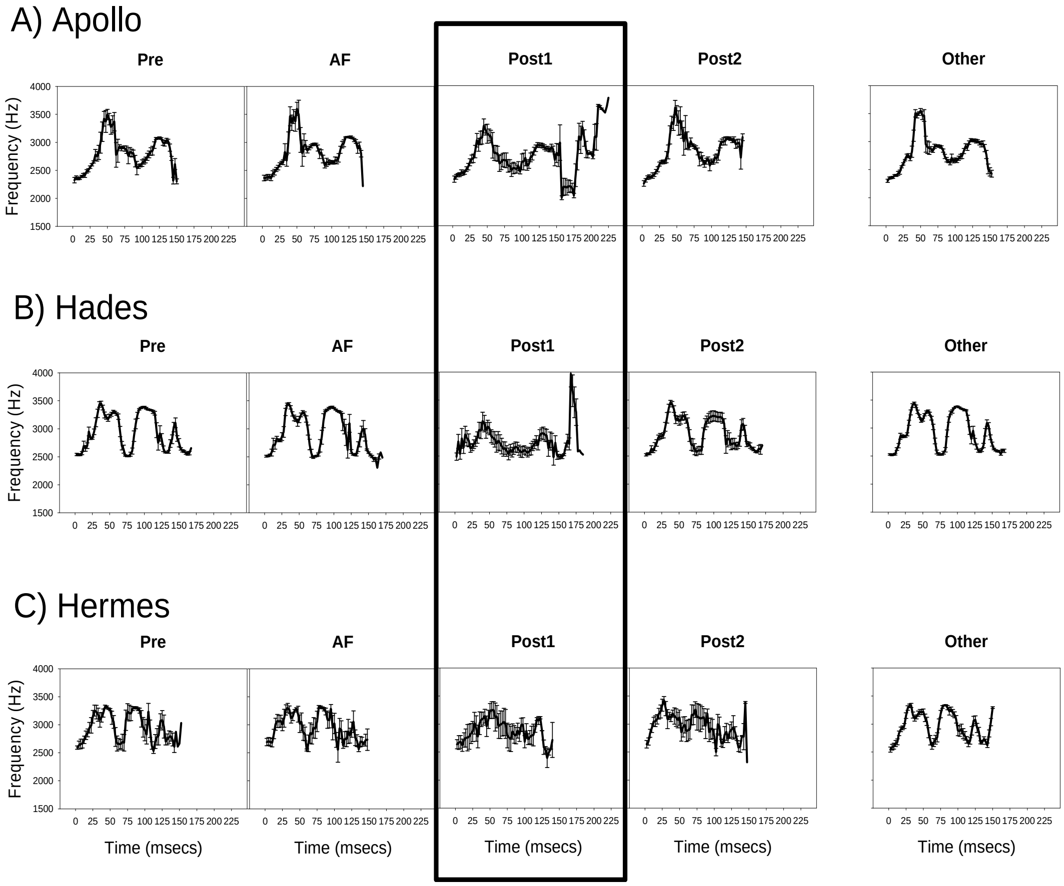

Figure 14. Average frequency contours from calls produced during the 25 ms delay sessions. Shown are the pre-feedback, feedback, and two post-feedback trials for those cases in which an error was produced during the 25 ms delay sessions. The average frequency contours for the remaining trials are also shown for comparison. Changes in the contours occurred primarily in the first post-feedback trial (boxed area) and appeared as an increase in variability (larger standard deviations), a decrease in frequency, a loss of frequency modulation (seen as a general flattening of the contours), and a change in duration. These changes largely disappeared by the second post-feedback trial.

feedback [Post1], second trial post-feedback [Post2], and all other trials [Other]) in the 25 millisecond delay sessions. Changes in the contours are most obvious in the Post1 trial (Figure 14, boxed area) and appeared primarily as an increase in frequency variance (larger standard deviations), an overall decrease in both frequency structure and overall frequency range (seen as a general flattening of the contours), and a change in duration. These changes had largely disappeared by the Post2 trial and were not noticeable in the contours from the other three trial types.

Importantly, these errors did not occur in real-time during feedback delivery but, instead, occurred primarily in one of the two subsequent vocalizations (83.0% of all errors occurred in the two calls following feedback). No errors occurred on the feedback trial itself. These results are consistent with those from Chapter 3 (Fletcher effect), but very different from the human and songbird cases in which DAF produces rapid changes to ongoing vocal behavior. This suggests that these birds may rely on AF in a very different way compared to other vocal learners.

IV. EXPERIMENT 2: REVERSED/OTHER CALL AUDITORY FEEDBACK

A. Method

1. Subjects

The three birds from Experiment 1 were used in this experiment.

C. Procedure

We used two different feedback stimuli in this experiment: A temporally-reversed version of the birds' trained call and another bird's contact call. In the 'other call' sessions, each subject received one of the other subject's calls as feedback and, therefore, had prior experience with hearing the feedback call. Stimuli were stored in a memory buffer in the TDT RP2.1. The RP2.1 immediately triggered playback of one of the feedback stimuli through the earphones when a vocalization was detected at the microphone. As in Experiment 1, the sound pressure level of the feedback was set as close to 70 dB SPL at each bird's ear as possible, as measured by a Larson-Davis Model 824 Sound Level Meter.

Birds were run in two sessions per stimulus type (i.e., reversed/other). Only one of the two feedback stimuli were used per session. Each session was comprised of 70 trials: 10 feedback trials and 60 non-feedback (quiet) trials. Feedback trials were randomized across a session such that one feedback trial was presented approximately every 3-8 trials. All vocalizations were stored digitally and analyzed off-line using procedures similar to those in Experiment 1. Briefly, all calls were first sorted by trial type and then average acoustic measures from each trial type were derived for each bird, including peak frequency, amplitude, duration, and similarity to template.

As in Experiment 1, contact calls were classified as "errors" based on one or more of the following criteria: 1) a correlation (similarity to template) value below 60%, 2) an average frequency differing by more than 250 Hz from the average frequency of a subject's trained call, and/or 3) a duration that was 20% longer or shorter than the average duration of a subject's trained call. In a typical training session for these subjects, the average similarity score was higher than 70%, the average frequency varied by < 100 Hz, and the duration varied by < 7%. Errors, as defined here, are typically rare occurrences.

C. Results and Discussion of Experiment 2

Several of the subjects' vocalizations were disrupted in this experiment (see Figure 13, right panel). There was a total of 60 feedback trials for each stimulus type (20 per subject) and 24 errors were produced as a result (the three birds produced 11, 10, and 3 errors; see below for a further description of error rates).

Errors were similar to those reported in the first experiment and were therefore classified using the same rubric as before (see Table 3, right column). We grouped errors into Error I (i.e., call elements added to or subtracted from a bird's trained call), Error II (i.e., a different call-type), or Error III categories (i.e., vocalizations which did not resemble a contact call). As before, Error II vocalizations were the most common (58.3% of all errors), followed by Error I (33.3% of all errors) and, finally, Error III (8.3% of all errors) vocalizations. As in Experiment 1, classification of a vocalization as Error I was at least partially dependent on differences in duration between errors and trained calls. Again, however, there was no significant difference in duration across birds because one subject produced errors which were longer than its trained calls (191.7 ms to 149.0 ms, respectively) while another bird produced errors which were shorter than its trained calls (124.9 ms to 146.5 ms, respectively). Error II vocalizations had a significantly lower correlation, peak frequency, and 3 dB bandwidth compared to trained contact calls. Only one bird produced Error III vocalizations in this experiment (N=2). These calls were therefore not analyzed, although they were lower in average similarity to template compared to that bird's trained calls ($r = 0.49$ vs. $r = 0.78$, respectively).

Error rates were similar to those reported in Experiment 1. There was no difference in error rate between either the 'reversed call' or the 'other call' stimulus conditions (Paired samples t-test; t[2] =-2.00, p = 0.18). Again, as in Experiment 1, errors tended to be produced within the first two trials following altered AF: 75.0% of all errors occurred within the first two calls after a feedback trial across both conditions and, of those errors, 66.7% occurred on the first call following feedback. There was also no difference in the error rate between the first and last half of a session (Paired samples t-test; t[2] =-1.42, p = 0.29).

These results show that gross spectrotemporal alterations to AF disrupt normal vocal production in budgerigars. Vocal disruptions primarily involved changes to the acoustic structure (as indicated by a lower similarity to template) and peak frequency of calls. Most (75.0%) of these errors occurred in one of the two vocalizations following an altered AF trial. This suggests that budgerigars attend to the overall spectrotemporal structure of AF and use received feedback to guide subsequent vocal production. As in Experiment 1, however, these results are different from those reported in songbirds, where altered AF produces rapid changes to ongoing vocal behavior.

V. GENERAL DISCUSSION

These results show that, as in humans and songbirds, budgerigars rely on the spectrotemporal pattern of AF to produce normal vocal behavior. The present experiments show that delaying or reversing the AF of a bird's call or providing another bird's call as feedback all have disruptive effects on vocal production in budgerigars. For DAF, there is a maximally-disruptive delay length that generates the most vocal errors and longer delays produced comparatively fewer errors. The most effective delay in the current study was 25 milliseconds (49.6% of all DAF errors occur at this delay). Human and songbird vocal responses to these kinds of alterations primarily involve a range of production errors. We report similar changes in budgerigar vocal behavior, including changes in peak frequency, amplitude, and duration. By far the most significant changes were seen in the spectrotemporal structure of disrupted calls compared to trained calls, measured as a decrease in similarity to a call template.

Errors generally fell into three categories: Error I vocalizations, in which call elements were added or subtracted from a bird's trained call, Error II vocalizations, in which the bird produced a different call-type, and Error III vocalizations, in which the bird produced a vocalization that did not resemble a complete contact call. In both experiments, the second kind of error (Error II) was the most common, followed by Error I and, finally, Error III vocalizations. Importantly, these errors did not occur in real-time during feedback delivery but, instead, occurred primarily in one of the two subsequent vocalizations. Errors did not occur on the feedback trial itself.

The majority of errors were made on trials immediately following feedback trials. This is consistent with results from Chapter 3 showing that amplitude adjustments do not occur in real-time but instead occur on the subsequent call. Based on these results, we present two scenarios describing potential mechanisms underlying this ballistic call production in budgerigars. First, contact calls may simply be too short to be affected by AF alterations in real-time. Delayed auditory feedback effects in humans and songbirds occur at delays of about 200 ms (e.g., Howell and Archer, 1984; Yates, 1963) and 100 ms (Cynx and Von Rad, 2001; Sakata and Brainard, 2006), respectively. This is about the duration of a typical budgerigar contact call and suggests that the physiological response to altered AF may require a minimum latency greater than the length of a call.

A second hypothesis is that contact calls cannot be modified online once initiated. Most of the errors in the current experiment do not appear to be instances in which the template call was simply halted during production, as is the case with studies of interruptibility in vocal production in other species (e.g., Cynx, 1990; Miller *et al.*, 2003), but instead seemed to be different, intact call-types (i.e., Error I and II vocalizations). This might result if incorrect AF served to disrupt selection of the correct motor program sequence giving rise to the next call-type rather than to disrupt ongoing call production itself. Onset delays for altered AF responses in songbirds are roughly equal to the average length of song syllables, which are themselves single vocal motor gestures and probably produced ballistically (Cynx, 1990; Franz and Goller, 2002; Riebel and Todt, 1997). However, budgerigars learn new calls through a process of recombination and modification of smaller call elements (Farabaugh *et al.*, 1994; Manabe and Dooling, 1997), suggesting that calls are actually quite plastic. Thus, it is unclear whether the lack of evidence for real-time adjustments reflects an interruption in motor sequencing or a physical constraint caused by the short duration of contact calls in these birds.

The physiological mechanisms underlying the DAF effect in humans have only recently begun to be explored. For example, there is evidence for vocalization-induced suppression of auditory cortex neural activity during ongoing speech (e.g., Houde *et al.*, 2002). This inhibition is believed to reflect an ‘error detection’ process whereby incoming auditory feedback is subtracted from an expectation of that auditory feedback. If the actual feedback matches expected feedback, the two signals cancel each other out. Consistent with this hypothesis, recent functional imaging studies have shown that altered auditory feedback, including DAF, activates areas in and around auditory cortex, superior temporal lobe, and planum temporale within 100-130 milliseconds during speech (Hashimoto and Sakai, 2003; Guenther, 2006). These findings support the idea that deviations from expected feedback are processed in these cortical areas. Similar patterns of excitation and suppression have been described more recently in non-human primates and may result from common mechanisms (e.g., Eliades and Wang, 2008).

Evidence shows that songbirds process vocal errors in forebrain areas. Sakata and Brainard (2006) showed that DAF of single song syllables provided to Bengalese finches resulted in vocal errors. Effective delays were as short as 20 milliseconds, although the most effective were 40 – 65 milliseconds. Also, errors did not occur within a syllable, but instead in subsequent syllables. The authors hypothesized that, based on these results, auditory feedback in these songbirds did not utilize a simple feedforward mechanism but instead served to guide syllable circuitry from one state to the next during song production. The authors also speculated that the feedback signal reaches the forebrain premotor nucleus HVC, which receives auditory input and is involved in syllable sequencing. A more recent study has shown that HVC contains a population of neurons that are activated by hearing a song and producing the same song (Prather *et al.*, 2008). These neurons project to striatal nuclei known to play a role in song learning and thus could be the site of comparison between expected and actual song feedback.

The physiological underpinnings of budgerigar vocal feedback control are much less understood than either humans or songbirds. Nucleus NLc, a telencephalic vocal motor region possibly analogous to songbird HVC, responds to auditory input with latencies of about 100 milliseconds (Plummer and Streidter, 2000) and projects to striatal structures responsible for learning new contact calls (Brauth et al., 1997; Streidter 1994). We hypothesize that this nucleus, if functionally similar to songbird HVC, might contain a population of neurons responsible for comparing actual and expected feedback, and could also be responsible for selecting the correct contact call circuitry prior to production. Because NLc would not receive AF until 100 milliseconds after vocal onset, it is not surprising that altered feedback cannot be used for online vocal corrections to short sounds. Interestingly, feedback does affect subsequent vocalizations as shown by the behavioral data described in this paper. In addition, if NLc guides selection of the correct circuitry underlying call production, DAF might also result in erroneous call selection or the production of alternate call-types. This is also consistent with the results of the present behavioral experiments.

Taken together, these findings suggest differences between DAF in humans and budgerigars. Recall that the average interval between trials, and thus between subsequent calls, was three to five seconds, much different than the case in humans and songbirds in which feedback disrupted ongoing vocalizations. In other words, altered feedback in budgerigars serves to disrupt call production over much longer time scales than previously reported in other vocal learning species. It is unclear what the neural underpinnings of this effect are.

In sum, these results show that AF in budgerigars, as in humans and songbirds, is used to guide future vocal production. Temporally- and spectrally-misaligned feedback received during call production interrupts subsequent calls. This differs from both the human and songbird cases in which AF is used to make online adjustments to vocalizations as they are produced and suggests that different mechanisms may underlie auditory monitoring of vocal production between these different groups of vocal learners.

Acknowledgments

We thank Elizabeth Brittan-Powell and Peter Marvit for comments on the manuscript. We also thank Leah Dickstein for help in performing the experiments. This work was supported by NIH grant DC-00198 to RJD, NIH grant DC-04664 to RJD, & NIH grant DC-006766 to MSO.

References

Bloodstein, O. (**1995**). *A handbook on stuttering* (National Easter Seal Society, Chicago, IL).

Brainard, M. S., and Doupe, A. J. (**2000**). "Auditory feedback in learning and maintenance of vocal behaviour," Nature Reviews. Neuroscience 1, 31-40.

Brauth, S. E., Heaton, J. T., Shea, S. D., Durand, S. E., and Hall, W. S. (**1997**). "Functional anatomy of forebrain vocal control pathways in the budgerigar (*Melopsittacus undulatus*),"Proc. NY Acad. Sci., 807, 368-385.

Brittan-Powell, E. F., Dooling, R. J., and Farabaugh, S. M. (**1997**). "Vocal development in budgerigars (*melopsittacus undulatus*): Contact calls," J. Comp. Psychol. 111, 226-241.

Brockway, B. F. (**1964a**). "Ethological studies of the budgerigar (*melopsittacus undulatus*): Non-reproductive behavior," Behavior 22, 193-222.

Brockway, B. F. (**1964b**). "Ethological studies of the budgerigar (*melopsittacus undulatus*): Reproductive behavior," Behavior 23, 294-324.

Brockway, B. F. (**1969**). "Roles of budgerigar vocalization in the integration of breeding behavior," in *Bird vocalizations*, edited by R. A. Hinde (Cambridge University Press, London), pp. 131-158.

Brown, S. D., Dooling, R. J., and O'Grady, K. (**1988**). "Perceptual organization of acoustic stimuli by budgerigars (*melopsittacus undulatus*): Iii. Contact calls," J. Comp. Psychol. 102, 236-247.

Chase, R. (**1965**). "An information-flow model of the organization of motor activity i: Transduction, transmission, and central control of sensory information," Journal of Nervous and Mental Disorders 140, 239-251.

Cynx, J. (**1990**). "Experimental-determination of a unit of song production in the zebra finch (*taeniopygia guttata*)," J. Comp. Psychol. 104, 3-10.

Cynx, J., and Von Rad, U. (**2001**). "Immediate and transitory effects of delayed auditory feedback on bird song production," Anim. Behav. 62, 305-312.

Dent, M. L. and Dooling, R. J. (**2003a**). "Investigations of the precedence effect in budgerigars: Effects of stimulus type, intensity, duration, and location," J. Acoust. Soc. Am., 113(4), 2146-2158.

Dent, M. L. and Dooling, R. J. (**2003b**). "Investigations of the precedence effect in budgerigars: The perceived location of auditory images," J. Acoust. Soc. Am., 113(4), 2159-2169.

Dent, M. L. and Dooling, R. J. (**2004**). "The precedence effect in three species of birds (*Melopsittacus undulatus, Serinus canaria*, and *Taeniopygia guttata*)," J. Comp. Psychol., 118(3), 325-331

Doupe, A. J., and Kuhl, P. K. (**1999**). "Birdsong and human speech: Common themes and mechanisms," Annu. Rev. Neurosci. 22, 567-631.

Eliades, S. J. and Wang, X. (**2008**). "Neural substrates of vocalization feedback monitoring in primate auditory cortex," Nature, Advance online publicaton May 4, 2008.

Fairbanks, G. (**1954**). "Systematic research in experimental phonetics i: A theory of the speech mechanism as a servosystem," Journal of Speech & Hearing Disorders 19, 133-139.

Fairbanks, G. (**1955**). "Selective vocal effects of delayed auditory feedback," Journal of Speech & Hearing Disorders 20, 333-346.

Farabaugh, S., and Dooling, R. J. (**1996**). "Acoustic communication in parrots: Laboratory and field studies of budgerigars, *melopsittacus undulatus*," in *Ecology and evolution of acoustic communication in birds*, edited by D. E. Kroodsma, and E. H. Miller (Cornell University Press, Ithaca, NY), pp. 97-118.

Farabaugh, S. M., Brown, E. D., and Dooling, R. J. (**1992**). "Analysis of warble song of the budgerigar, melopsittacus undulatus," Bioacoustics 4, 111-130.

Farabaugh, S. M., Dent, M. L., and Dooling, R. J. (**1998**). "Hearing and vocalizations in native australian budgerigars (melopsittacus undulatus)," J. Comp. Psychol. 112, 74-81.

Farabaugh, S. M., Linzenbold, A., and Dooling, R. J. (**1994**). "Vocal plasticity in budgerigars (*melopsittacus undulatus*): Evidence for social factors in the learning of contact calls," J. Comp. Psychol. 108, 81-92.

Finney, S. A., and Warren, W. H. (**2002**). "Delayed auditory feedback and rhythmic tapping: Evidence for a critical interval shift," Perception & Psychophysics 64, 896-908.

Franz, M., and Goller, F. (**2002**). "Respiratory units of motor production and song imitation in the zebra finch," J Neurobiol 51, 129-141.

Guenther, F. H. (**2006**). "Cortical interactions underlying the production of speech sounds," Journal of Communication Disorders, 39, 350-365.

Hashimoto, Y. and Sakai, K. (**2003**). "Brain activations during conscious self-monitoring of speech production with delayed auditory feedback: An fMRI study," Human Brain Mapping, 20, 22-28.

Hile, A. G., Plummer, T. K., and Striedter, G. F. (**2000**). "Male vocal imitation produces call convergence during pair bonding in budgerigars, *melopsittacus undulatus*," Anim. Behav. 59, 1209-1218.

Hile, A. G., and Striedter, G. F. (**2000**). "Call convergence within groups of female budgerigars (*melopsittacus undulatus*)," Ethol. 106, 1105-1114.

Houde, J. F., Nagarajan, S. S., Sekihara, K., and Merzenich, M. M. (**2002**). "Modulation of the auditory cortex during speech: An MEG study," Journal of Cognitive Neuroscience, 14, 1125-1138.

Howell, P., and Archer, A. (**1984**). "Susceptibility to the effects of delayed auditory feedback," Percept. & Psychophys. 36, 296-302.

Konishi, M. (**2004**). "The role of auditory feedback in birdsong," in *Behavioral neurobiology of birdsong*, edited by H. P. Zeigler, and P. Maler (New York Academy of Sciences, New York), pp. 463-475.

Kroodsma, D. E., and Miller, E. H. (**1982**). *Acoustic communication in birds* (Academic Press, New York, NY).

Lee, B. S. (**1950**). "Effects of delayed speech feedback," Journal of the Acoustical Society of America 22, 824-826.

Leonardo, A., and Konishi, M. (**1999**). "Decrystallization of adult birdsong by perturbation of auditory feedback," Nature 399, 466-470.

Manabe, K., and Dooling, R. J. (**1997**). "Control of vocal production in budgerigars (melopsittacus undulatus): Selective reinforcement, call differentiation, and stimulus control," Behav Process 41, 117-132.

Miller, C. T., Flusberg, S., and Hauser, M. D. (**2003**). "Interruptibility of long call production in tamarins: Implications for vocal control," J Exp Biol 206, 2629-2639.

Nottebohm, F. (**1972**). "Origins of vocal learning," Am Nat 106, 116-140.

Plummer, T. K. and Streidter, G. F. (**2000**). " Auditory responses in the vocal motor system of budgerigars," J. Neurobiol., 42, 79-94.

Prather, J. F., Peters, S., Nowicki, S., and Mooney, R. (**2008**). " Precise auditory-vocal mirroring in neurons for learned vocal communication," Nature, 451, 305-310.

Riebel, K., and Todt, D. (**1997**). "Light flash stimulation alters the nightingale's singing style: Implications for song control mechanisms," Behaviour 134, 789-808.

Sakata, J. T., and Brainard, M. S. (**2006**). "Real-time contributions of auditory feedback to avian vocal motor control," The Journal Of Neuroscience: The Official Journal Of The Society For Neuroscience 26, 9619-9628.

Striedter, G. F. (**1994**). "The vocal control pathways in budgerigars differ from those in songbirds," J Comp Neurol 343, 35-56.

Striedter, G. F., Freibott, L., Hile, A. G., and Tyler Burley, N. (**2003**). "For whom the male calls: An effect of audience on contact call rate and repertoire in budgerigars, *melopsittacus undulatus*," Anim. Behav. 65, 875-882.

Tchernichovski, O., Mitra, P. P., Lints, T., and Nottebohm, F. (**2001**). "Dynamics of the vocal imitation process: How a zebra finch learns its song," Science 291, 2564-2569.

Yates, A. J. (**1963**). "Delayed auditory feedback," Psychol Bull 60, 213-232.

Chapter 5 - Effects of Differentially Reinforcing Pitch Changes

I. INTRODUCTION

Many animals actively control the pitch of their vocalizations. For example, great tits living in noisy urban areas raise the frequency of their song to avoid masking from anthropogenic noise (Slabbekoorn and Peet, 2003). The ability to precisely control pitch changes in song is a sexually-selected trait in black-capped chickadees (Cristie *et al.*, 2004). Some bats can make extremely precise, on-line adjustments to the frequency of their echolocation calls based on the frequency of the returning echo signal during flight (Metzner *et al.*, 2002; Smotherman *et al.*, 2003). This Doppler-shift compensation behavior of bats is one of the most precise forms of frequency control described in any species.

Budgerigars are small, highly social, gregarious parrots that have a complex, learned vocal repertoire (see review in Farabaugh and Dooling, 1996). We know budgerigars exert a level of fine control over their vocalizations based on sensory feedback. For example, they have control over the intensity of their vocal behavior and exhibit a robust Lombard effect (Manabe *et al.*, 1998 and also Chapter 3) and are sensitive to the timing and spectrotemporal pattern of auditory feedback (AF) (Chapter 4). Birds deafened as nestlings do not learn to produce the normal contact calls of hearing birds (Heaton and Brauth, 1999), and deafened adults show an inability to maintain precision in their vocal output (Dooling *et al.*, 1987; Dooling *et al.*, 1997; Heaton and Brauth, 1999). These studies show both call frequency and the production of learned frequency modulation patterns deteriorate severely in deafened animals. Budgerigars use pitch to discriminate the contact calls of individuals (Brown *et al.*, 1988) and call frequency in these birds remains relatively stable across multiple renditions of a call-type (Osmanski and Dooling, 2004). Thus, budgerigars likely have internal control over the frequency structure of their calls which is guided by AF.

Budgerigars learn new calls in a rich social environment, but examining call learning in such an environment is complicated by a lack of control over the precise acoustic, visual, and social experiences of the individuals under study (see Farabaugh *et al.*, 1994). We know that vocal production can be brought under stimulus control in an operant environment (e.g., Manabe and Dooling, 1997; Manabe *et al.*, 2008; Manabe *et al.*, 1995; Manabe *et al.*, 1997), and experiments using differential reinforcement as a proxy for social reinforcement may provide a more fruitful avenue for studies of call learning and call modification in these birds. Thus, operant experiments can be used to probe the limits of, and look into potential constraints on, vocal production in these birds.

Results from Chapter 3 and Chapter 4 show that birds do not make real-time adjustments based on altered AF and instead suggest that contact calls may be produced in a ballistic fashion. One potential implication of this is that contact calls could represent irreducible vocal motor units akin to birdsong syllables (e.g., Cynx, 1990; Franz and Goller, 2002; Riebel and Todt, 1997) and, thus, individual call segments cannot be modified relative to other segments. Instead, the entire global call structure must be changed wholesale. Other data, however, show that budgerigar contact calls do change in structure over time and that these changes do not occur across an entire call but, instead, occur only in certain call segments (e.g., Chapters 2 and 3; Brittan-Powell *et al.*, 1997; Farabaugh *et al.*, 1994). For example, results from Chapter 2 in this dissertation showed subtle changes in the terminal segments of some calls that accrued over the course of several weeks. Results from Chapter 3 showed changes to the frequency (and amplitude) structure of certain call segments, but not others, when making adjustments to call amplitude in response to changes in the level of auditory feedback. Also, Farabaugh and colleagues (1994) described subtle, improvised changes in the frequency pattern of particular call elements during weekly recording sessions.

Here we performed two experiments to examine whether, to what extent, and in what ways, budgerigars can modify the frequency structure of their calls. These experiments address the limits of plasticity in the frequency parameters of these calls. The first experiment tested whether these birds could change the overall frequency of their calls when constrained to maintain the overall spectrotemporal pattern (i.e., birds were required to match a stored call template call as that template was shifted upward in frequency within a test session). A second experiment allowed unconstrained changes by reinforcing any frequency change regardless of whether the bird preserved the spectrotemporal pattern of its call (i.e., birds were not required to match a stored template). We hypothesized, based on previous results (e.g., Chapter 2; Brittan-Powell *et al.*, 1997; Farabaugh *et al.*, 1994), that birds in these experiments would require several sessions to alter the frequency of their calls and those alterations would entail changes in call structure.

II. GENERAL METHODS

A. Subjects

The subjects in these experiments were four adult budgerigars from a colony maintained in an aviary at the University of Maryland. Each bird was separately caged and had *ad libitum* access to water. Since food was used to reinforce vocal behavior, the birds were maintained at 90% of their free-feeding body weight. The University of Maryland Animal Care and Use Committee approved all experimental procedures.

B. Apparatus

Birds were trained in an operant testing apparatus consisting of a small wire cage (14 cm x 12 cm x 17 cm) constructed of wire mesh and mounted in an acoustic isolation chamber (Industrial Acoustic Company model AC-1). Three light-emitting diodes (left, center, and right LEDs) were attached to a piece of anechoic foam on the front panel of the cage at approximately the level of the bird's head. Three small speakers (SONY model MDR-Q22LP) were mounted on the exterior of the cage – one at the center above the front LED panel and one on each of the left and right sides. A small directional microphone (SONY model ECM-77B), located just below the LED panel, detected vocalizations. A food hopper containing hulled millet was located on the floor of the cage under the front LED panel. A small video camera was used to monitor the bird's behavior while in the chamber. See Figure 3 for an image of this operant setup.

C. Training/Testing Procedure and Analysis

1. Contact Call Detection & Analysis

Training/testing and analysis programs were generated using MATLAB software and Tucker Davis Technologies (TDT) System III hardware (Gainesville, FL). The output of the microphone was amplified, low-pass filtered at 10 kHz, and sent to a circular memory buffer in a TDT real-time digital signal processor (RP2.1) at a nominal sampling rate of 25 kHz. A typical budgerigar contact call has a duration of 100-150 milliseconds and spectral energy concentrated between 2-4 kHz (Farabaugh and Dooling, 1996; Farabaugh *et al.*, 1998; Farabaugh *et al.*, 1994). Therefore, incoming signals were classified as a contact calls if signal intensity exceeded a user-defined value for a minimum of 70 milliseconds and if, during this time, the signal power in the frequency band between 2 and 4 kHz exceeded that measured between 4 and 10 kHz.

All signals classified as contact calls were sent to MATLAB and saved for later analysis. Analysis involved: 1) generation of power spectra iteratively across each call in 5 ms windows (with 50% window overlap), 2) measurement of several acoustic parameters from these power spectra, including average peak frequency, average peak amplitude, and 3 dB bandwidth of the spectral peak, and 3) calculation of whole-call measurements, including Wiener entropy (a unitless measure of disorder, see Tchernichovski *et al.*, 2001) and a similarity measure of the call to a to-be-matched template call (see sections 3 and 4 below for a description of the template and correlation algorithm). Also, peak frequency and peak amplitude contours, along with total power spectra, were saved for each call. These measures were analyzed using SPSS software.

2. Initial Training (Shaping)

Birds were first habituated to the experimental chamber and trained to eat from the food hopper when it was activated. Once the birds consistently ate from the raised hopper, manual shaping of vocalizations began. Here, typical aviary sounds were played in the operant chamber to induce the birds to vocalize. Whenever the birds responded to the aviary tape with a contact call, the experimenter activated the hopper. Birds quickly came to associate vocalizing in the test chamber with access to food and, therefore, tape playback was phased out over several training sessions. When birds reliably produced contact calls in the absence of the aviary tape, vocal behavior was reinforced automatically.

Birds were next trained to vocalize only when the center LED was illuminated. Here, the LED turned off each time a vocalization was acquired and turned on again after a random time interval (approximately 5-15 seconds). Only vocalizations produced when the light was illuminated were reinforced. Vocalizations produced when the LED was turned off caused the random interval timer to reset and increased the wait time before the LED turned back on. Birds successfully completed this phase of training when they reliably vocalized in the chamber both without the flock tape and only in response to the illuminated center LED.

3. Contact Call Recognition

After completing the previous phase, birds were tested in several further training sessions to establish a call repertoire. The most typical contact call in a bird's repertoire was selected as that bird's "template" call (see Manabe and Dooling, 1997). A spectral cross-correlation program generated a similarity index between all calls produced in these sessions. This program created a spectrogram for each signal using a 256-point Hanning window with 50% window overlap. These spectrograms were then compared using a MATLAB 2-dimensional cross correlation algorithm (MATLAB function XCORR2). This algorithm generated a series of correlation values representing all possible temporal offsets between the two spectrograms. The maximum correlation value was taken as the similarity index between the two calls. This similarity index was then normalized so that it was zero if two calls were perfectly dissimilar and one if the calls were identical. A matrix of similarity values was constructed from all calls produced in a test session and was analyzed using a MALAB classical multidimensional scaling algorithm. The call in the center of the largest cluster in this two-dimensional space was selected as the template call for the next phase of training.

4. Template Training (Precision)

Subsequent training sessions used this template call in order to differentially reinforce vocal behavior. Birds were rewarded only for producing calls that were similar to the template call (using the same spectral cross-correlation algorithm described above). Every vocalization produced by a bird was compared to the stored digital template in real-time. The bird was reinforced if the correlation between the two calls exceeded a user-defined value. No reward was given if the correlation did not exceed this value. At first, the criterion correlation value was set very low (e.g., r= .01) so that all calls were reinforced. The criterion was gradually increased over several sessions to a maximum value of r = .70. All training sessions were terminated after 50 reinforcements or 25 minutes, whichever came first. Subjects were tested in two daily sessions, five days per week. All test sessions were separated by at least three hours.

III. EXPERIMENT 1: CONSTRAINED FREQUENCY CHANGE

A. Methods

1. Subjects

Three adult budgerigars (2 male, 1 female) were used in this experiment.

B. Procedure

Once the birds were trained to asymptotic levels of performance on the template-training task described above, a new testing phase was introduced. For this phase, each bird's stored template call was shifted upward in frequency offline by either 50 Hz or 100 Hz using a MATLAB spectral-shifting program. This raised the overall frequency of the entire call while preserving its original spectrotemporal structure.

Birds were tested in five sessions at each of the three shift magnitudes (i.e., 50 Hz, 100 Hz, and unshifted [0 Hz]). Each session followed an A-B-A experimental design. At the beginning of each test session (A1 trials), all contact calls were compared to the original, unshifted template and birds were only rewarded for producing contact calls that matched the template (i.e., $r > .70$). After 15 reinforcements, the stored template was changed to one of the two frequency-shifted templates (B trials; the unshifted, original template was used in control sessions). Birds were now required to produce calls that matched the new template (i.e., $r > .70$). Thus, in order to be reinforced, each bird had to both raise the frequency of its entire call while simultaneously preserving its spectrotemporal structure. After 15 additional reinforcements, the stored template was switched back to the original template for a final 15 reinforcements (A2 trials). Sessions were terminated after 45 total reinforcements (i.e., 15 reinforcements in A1 trials [unshifted template], 15 reinforcements in B trials [shifted template] and 15 reinforcements in A2 trials [unshifted template]) or after 25 minutes, whichever came first.

All vocalizations were stored digitally and analyzed off-line using a signal analysis program written in MATLAB. Analysis involved a two-step process in which calls were first sorted by trial type (i.e., A1 [unshifted template] vs.B [shifted template] vs. A2 [unshifted template]). Step two involved an acoustic analysis of calls within each trial type. Acoustic measures included peak frequency and similarity to template. Additionally, peak frequency contours were generated to facilitate comparisons among the different trial types.

C. Results and Discussion of Experiment 1

All three birds showed significant performance deficits during sessions in which they were required to increase the frequency of their calls. Percentage of reinforced calls (out of all calls produced) dropped significantly across sessions, from 86.5% in the control sessions (e.g., 0 Hz shift) to 60.7% in the 50 Hz shift sessions to 34.4% in the 100 Hz shift (One-way RM ANOVA; $\underline{F}(2,4) = 32.1$, $\underline{p} < 0.01$). Importantly, only one bird was able to successfully complete 45 reinforced calls in the 100 Hz template shift sessions. The other two birds stopped behaving as a result of not being reinforced often enough and their sessions were terminated because the time limit was exceeded. Therefore, remaining analyses were only performed for the

0 Hz template shift and the 50 Hz template shift sessions. Data from the 100 Hz sessions from this one subject are provided for comparison purposes only.

All three birds produced significantly more unreinforced calls (i.e., calls that did not match the template; Figure 15A, left panel) and showed a concomitant decrease in similarity to the call template (Figure 15B, left panel) across trial types (i.e., A1-B-A2) in the 50 Hz shift sessions, but not in the 0 Hz shift sessions (see Table 4). In other words, birds were not able to match the template well when it was raised by 50 Hz. There were no differences across trials in either shift session for average frequency (Figure 15C, left panel) (Table 4). Additionally, there were no differences between the two unshifted template trial conditions (i.e., A1 and A2) in either the 0 Hz or the 50 Hz shift sessions (see Table 5), suggesting that the birds had not made within-session adjustments to their calls. Single subject data from the 100 Hz sessions are provided in the right-hand panels of Figure 15 for comparison. Performance for this bird is as bad as or worse than in the 50 Hz session (i.e., greater number of unreinforced calls and a low similarity measure).

Figure 16 shows the average frequency contours of the reinforced calls (i.e, those calls that matched the shifted template) produced during the B trials (i.e., when the template was raised by 0 Hz or 50 Hz, respectively) for all three subjects. The birds did not change the structure of their calls within a session. Single subject data from the 100 Hz sessions are provided in the right-hand panel of Figure 16B for comparison. Again, the two call contours appear largely identical, which suggests that the bird had made no attempt to adjust its call structure.

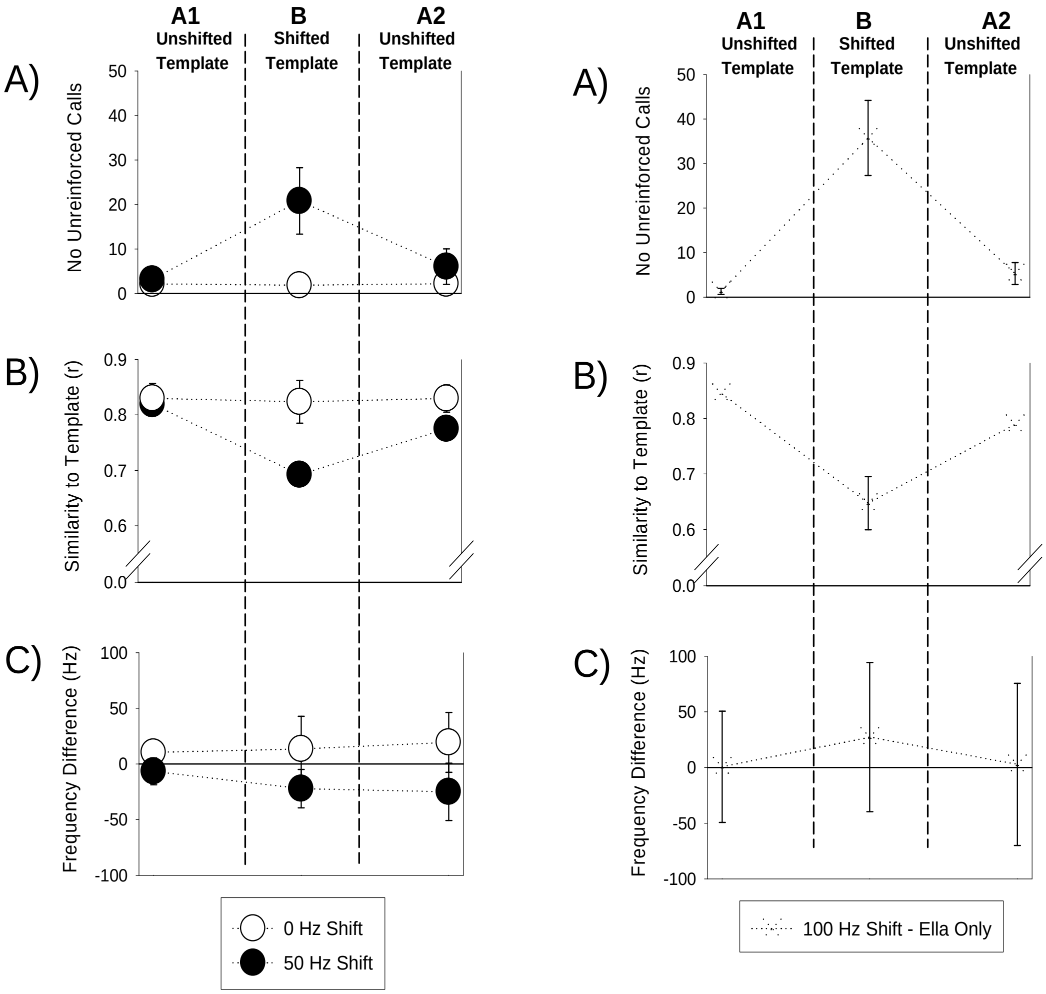

Figure 15. Performance deficits during sessions in which birds were constrained to match a shifted template. Left panels show data from all three birds in the 0 Hz shift and 50 Hz shift sessions. Right panels show data from the one bird that completed the 100 Hz sessions for comparison purposes. <u>A, left panel)</u> The number of non-reinforced calls (i.e., calls which did not match the template) produced across each session increases significantly when the template is shifted 50 Hz. There was no difference between the A1 and A2 conditions for either shift amount. <u>B, left panel)</u> Average similarity to template decreases significantly when the template is shifted 50 Hz. Again, there was no difference between the A1 and A2 conditions for either shift amount. <u>C, left panel)</u> Average peak frequency of calls produced across each session does not change with increasing shift magnitude.

Table 4. Changes Across A1-B-A2 Trials in 0 Hz and 50 Hz Template Shift Sessions

	0 Hz Shift		**50 Hz Shift**	
Acoustic Measures	**F (2,4)**	**Significance**	**F(2,4)**	**Significance**
No. Unreinforced Calls	0.84	0.92	**25.5**	< **0.01**
Spectral Cross-Correlation	2.06	0.29	**23.2**	< **0.01**
Frequency	0.85	0.49	2.78	0.18

Measures in **BOLD** are significantly different across sessions

Table 5. Changes Between A1 and A2 Trials in 0 Hz and 50 Hz Template Shift Sessions

	0 Hz Shift		**50 Hz Shift**	
Acoustic Measures	**t (2)**	**Significance**	**t(2)**	**Significance**
No. Unreinforced Calls	-0.42	0.97	-1.23	0.34
Spectral Cross-Correlation	0.346	0.77	1.99	0.19
Frequency	-1.00	0.42	0.34	0.77

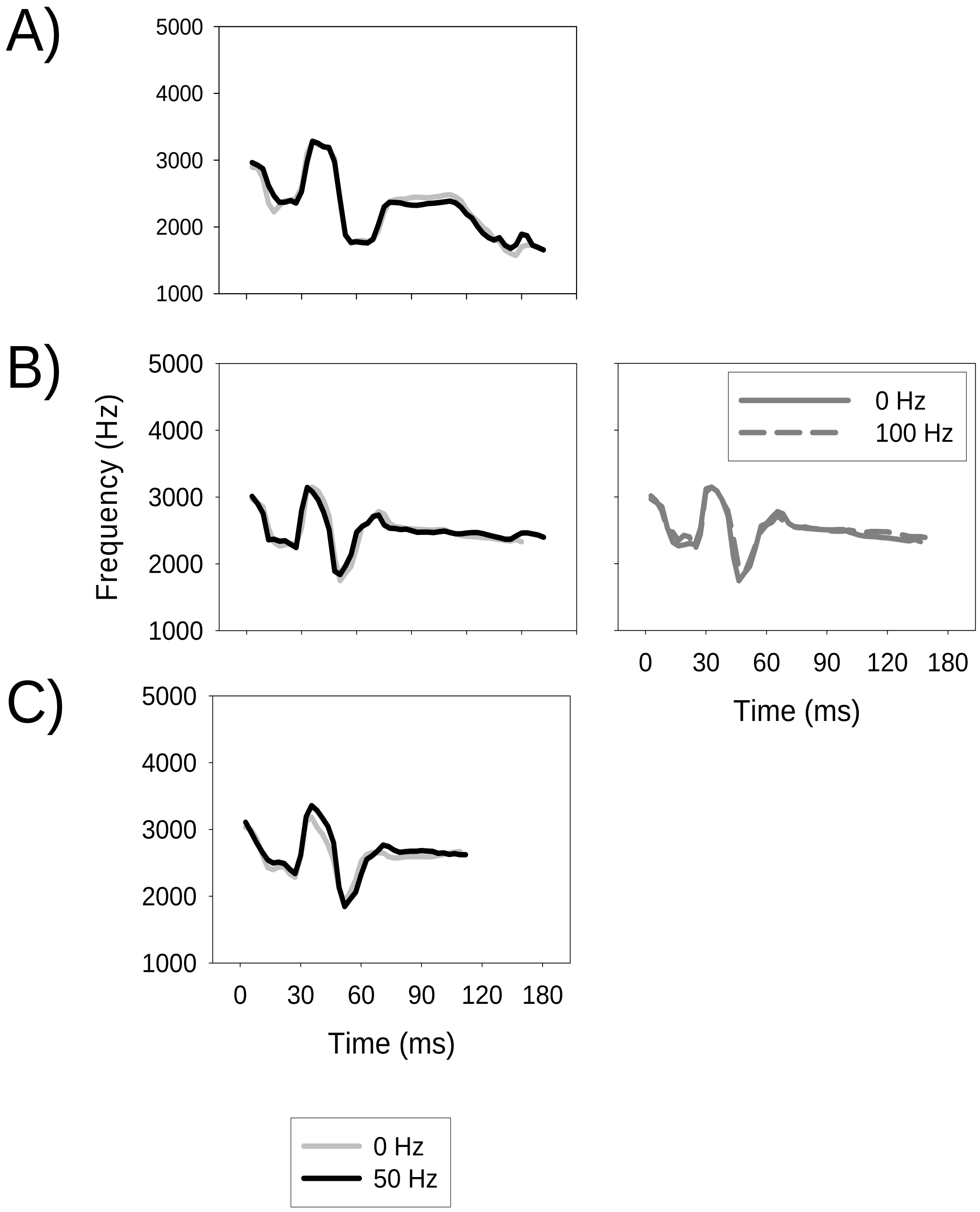

Figure 16 - Average peak frequency contours of reinforced calls for each of the three birds showing no obvious changes in call frequency. <u>Left panels</u>) Contours for each of the three birds (A - C) at 0 Hz and 50 shift magnitudes during B trials (i.e., trials in which the template was shifted). There were no obvious changes in call frequency for any of the three birds. <u>Right panel</u>) Average contours from the one bird that completed the 100 Hz sessions during B trials. Again, there were no obvious changes in call frequency.

These results suggest that budgerigars may not be able to change the frequency structure of their calls in a highly constrained way. Instead, they appear to have simply produced the same call over and over, being intermittently reinforced as a result of some calls being produced at a slightly higher pitch than others.

IV. EXPERIMENT 2: UNCONSTRAINED FREQUENCY CHANGE

The previous experiment showed that birds could not raise the frequency of their entire contact call when constrained to match a shifted template. Experiment 2 sought to determine whether they could do so if allowed to make unconstrained changes to the overall average frequency of their contact call across sessions.

A. Methods

1. Subjects

Four adult budgerigars (3 male, 1 female) were used in this experiment, including one male and one female from the previous experiment.

B. Procedure

Birds were tested in five baseline sessions of 50 trials each. These five sessions were identical to the template-training sessions above except that all vocalizations were reinforced whether or not they matched the template. Following these baseline sessions, a series of test sessions were conducted in which reinforcement was contingent upon the birds producing calls either higher or lower in average frequency than those produced in the final baseline session. Two of the birds were required to first increase, and then decrease, the average frequency of their calls while the other two birds were required to first decrease, and then increase, their call frequency. The general procedure for differentially-reinforcing a change in frequency was the same for increases and decreases in frequency. First, the average frequency of all calls produced in the final baseline session was calculated and used as either the minimum or maximum allowable frequency of each call produced in the next session. Birds were only reinforced if the average frequency of each call they produced was greater than (in the case of increasing frequency) or less than (in the case of decreasing frequency) this criterion value. The criterion was changed in the next session if at least 66% of the calls produced during a given session were rewarded. In this case, the new criterion value was set to the average frequency of all of the calls produced during the last session. These differential reinforcement sessions were terminated when a bird ran 10 successive sessions in which less than 66% of the calls were reinforced. The birds were then run in a second baseline series of five sessions during which all vocalizations were reinforced. All analyses of calls would be performed during the two series of baseline sessions, when there was no differential reinforcement driving vocal behavior.

All vocalizations were stored digitally and analyzed off-line using a signal analysis program written in MATLAB. Acoustic analysis included calls produced in the last session before, and the first session following, differential reinforcement of call frequency. Acoustic measures included similarity to template, average peak frequency, 3dB bandwidth, average amplitude, duration, and Weiner entropy. Additionally, peak frequency contours were generated to facilitate comparisons between the two sessions.

C. Results and Discussion of Experiment 2

All four birds successfully altered the average frequency of their contact calls to values well outside the typical range of variation measured in the initial baseline sessions (Figure 17). We measured significant increases (One-way RM ANOVA; $\underline{F}(1,199) = 378.5$, $\underline{p} < .001$) and decreases (One-way RM ANOVA; $\underline{F}(1,180) = 432.4$, $\underline{p} < .001$) in average call frequency between the sessions immediately preceding and immediately following differential reinforcement. After reaching asymptotic performance at a new frequency range, each bird continued to produce contact calls within this new frequency range even after all frequency requirements were removed (i.e., second baseline series, Figure 17). This behavior continued for all of the no-contingency sessions tested (5 sessions of approximately 250 calls for each bird).
All of the birds altered the spectrotemporal structure of their calls. In no case did a bird simply raise the frequency of the entire call without also making some structural modification to it. For example, one bird decreased its average frequency by lowering a terminal segment (i.e., Figure 18A) while another increased its average call frequency by raising an initial call segment (i.e., Figure 18B). Relatively large changes in frequency (>200 Hz) were always accomplished by making gross changes to a call's overall spectrotemporal structure (e.g., Figure 18B and 18C). These changes, measured by spectral cross-correlation, were significantly different for both increasing (One-way RM ANOVA; $\underline{F}(1,199) = 491.9$, $\underline{p} < .001$) and decreasing (One-way RM ANOVA; $\underline{F}(1,180) = 39.6$, $\underline{p} < .001$) frequency sessions.

Other acoustic measures also changed significantly. Increasing average frequency was associated with an increased 3dB bandwidth (One-way RM ANOVA; $\underline{F}(1,199) = 51.6$, $\underline{p} < .001$), increased amplitude (One-way RM ANOVA; $\underline{F}(1,199) =$

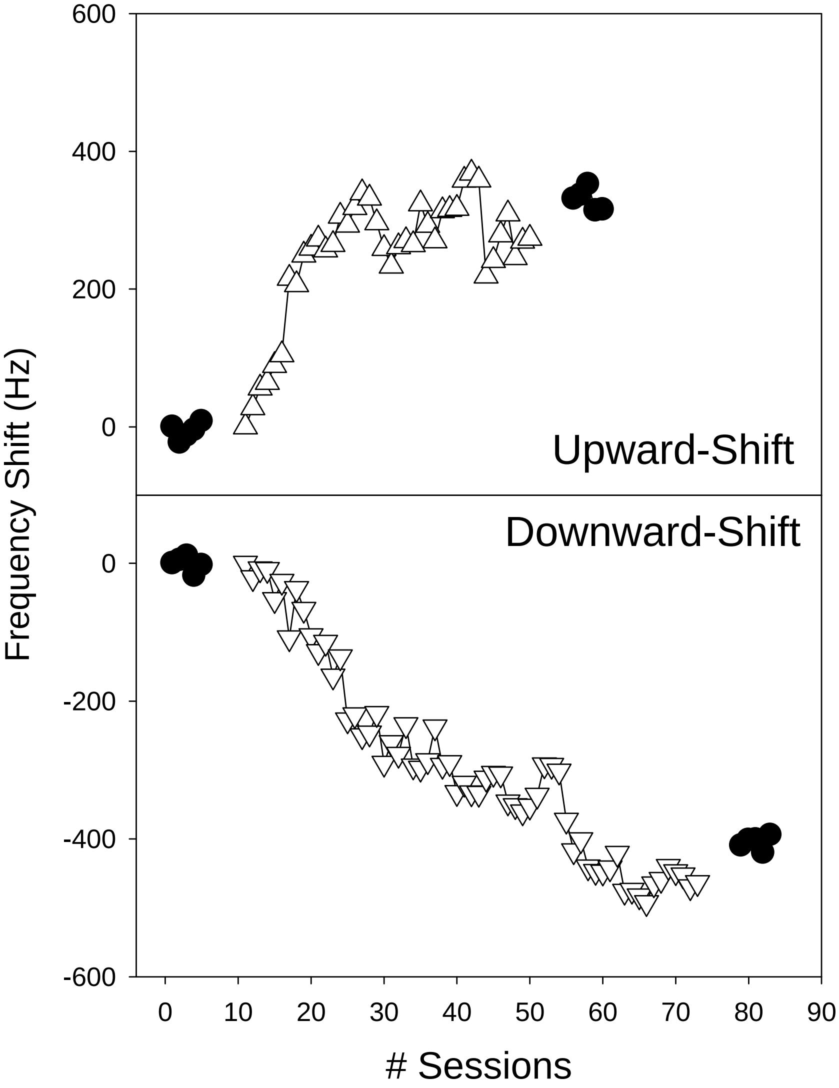

Figure 17. ̲Average vocal frequency shift measured when birds were allowed to make unconstrained frequency shifts The top panel shows changes in average frequency when birds increase the average frequency of their contact calls while the bottom panel shows similar when birds decrease their average call frequency. Closed circles denote baseline sessions with no differential reinforcement. Open circles denote sessions with differential reinforcement of increasing or decreasing vocal frequency. Data are plotted as difference values (measured as the change from the average frequency measured in the first baseline session).

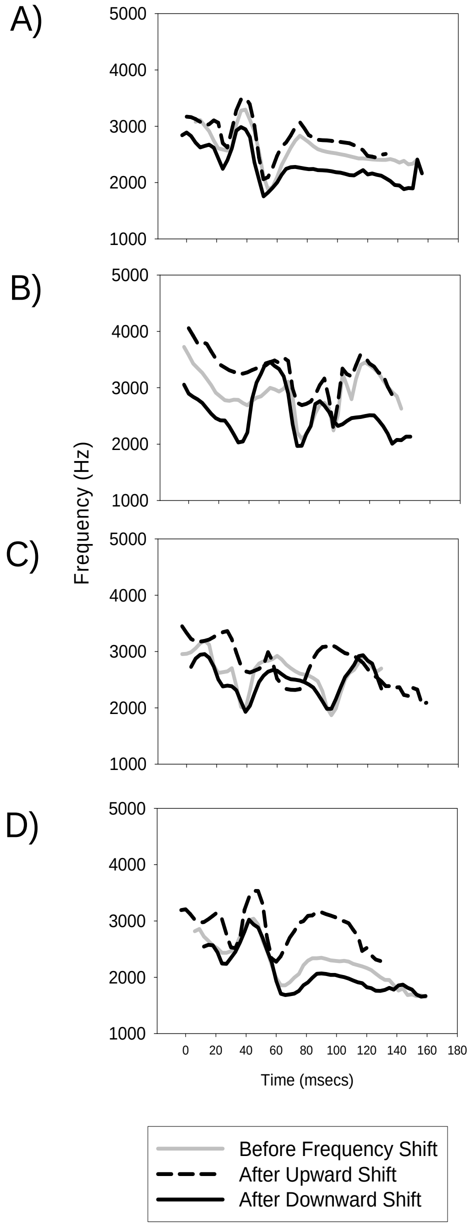

Figure 18. Average peak frequency traces showing the effect of increasing and decreasing frequency on call structure for each of the four birds. Comparisons are between the no-contingency endpoints of the experiment (i.e., before differential reinforcement of frequency changes (gray lines) and after differential reinforcement of frequency changes (black lines). Birds responded to differential reinforcement by altering the frequency structure of their calls. This modification usually occurred in certain call segments and sometimes resulted in gross changes to call structure.

77.4, $p < .001$), and decreased duration (One-way RM ANOVA; $F(1,199) = 5.3$, $p < .05$), but not Wiener entropy (One-way RM ANOVA; $F(1,199) = .512$, $p = .475$). Similarly, decreasing frequency is associated with concomitant changes to 3dB bandwidth (One-way RM ANOVA; $F(1,180) = 48.3$, $p < .001$) and amplitude (One-way RM ANOVA; $F(1,180) = 137.8$, $p < .001$), but not duration (One-way RM ANOVA; $F(1,199) = 1.56$, $p = .214$) or Wiener entropy (One-way RM ANOVA; $F(1,199) = 3.25$, $p = .073$).

V. GENERAL DISCUSSION

Here we performed two experiments to examine whether, to what extent, and in what ways, budgerigars can modify the frequency of their calls. The first experiment tested whether these birds would make changes to the frequency of their calls within a session when constrained to keep the overall spectrotemporal pattern of those calls. Budgerigars were unable to perform this task. Subjects showed performance deficits consistent with an inability to make adjustments to call frequency in the 50 Hz shift sessions and two of the three subjects ceased vocalizing entirely before completing the 100 Hz shift sessions. Frequency contours showed no obvious changes between shift sessions, suggesting that the birds had made no attempt to change call structure in this experiment.

A second experiment probed the limits of unconstrained frequency change across sessions when birds were not required to keep the same spectrotemporal call structure. Birds increased and decreased the frequency of their contact calls in this second experiment by several hundred Hz in each direction. Measured frequency changes remained well within the overall range of frequencies typical of this species

(1000 - 5000 Hz). There were also adjustments in several other acoustic parameters, including concomitant changes in 3dB bandwidth and peak amplitude and an inverse relationship with duration.

The largest, most obvious change was in the global spectrotemporal structure of the contact calls. None of the four birds simply raised or lowered the overall call contour. Instead, each bird made alterations to the acoustic structure of the call. Some birds raised particular call segments while others lowered call segments. These alterations resulted in gross changes to call structure when the average call frequency was changed by > 200 Hz.

These results point to potential constraints on vocal production in budgerigars and may speak towards the mechanisms underlying vocal behavior in these birds. Physical and motor constraints set boundaries on vocal development and production in songbirds – including the limiting effects of vocal tract oscillations on trill rate (Podos, 1996, 1997), beak size on syllable repetition rate and vocal frequency (Podos, 2001), and beak gape on frequency, amplitude, and harmonic structure (Goller *et al.*, 2004; Hoese *et al.*, 2000; Podos *et al.*, 2004; Westneat *et al.*, 1993). It is unclear whether, or to what extent, similar constraints may be operating in budgerigars which prevent birds from making pitch changes while preserving the overall spectrotemporal form of the call. It is also unclear whether a process of vocal self-monitoring is involved in these call alterations.

These results suggest that contact calls are comprised of a series of short acoustic elements that can each be modified relative to other segments. This is consistent with results from Chapter 2 and Chapter 3 showing changes in the frequency structure of certain call segments compared to others. These data also generally fit with previously-described mechanisms of call learning and development in these birds, which can occur through the modification of existing call elements (Brittan-Powell *et al.*, 1997; Farabaugh and Dooling, 1996; Farabaugh *et al.*, 1994; Manabe and Dooling, 1997; Manabe *et al.*, 2008). Thus, the changes in call structure that we report here appear to operate via a mechanism similar to that described for the formation of new calls and the modification of existing calls.

Acknowledgments

We thank Elizabeth Brittan-Powell and Peter Marvit for comments on the manuscript. We also thank Kevin Budman for help in performing the experiments. This work was supported by NIH grant DC-00198 to RJD, NIH grant DC-04664 to RJD, & NIH grant DC-006766 to MSO.

References

Brittan-Powell, E. F., Dooling, R. J., and Farabaugh, S. M. (**1997**). "Vocal development in budgerigars (*melopsittacus undulatus*): Contact calls," J. Comp. Psychol. 111, 226-241.

Brown, S. D., Dooling, R. J., and O'Grady, K. (**1988**). "Perceptual organization of acoustic stimuli by budgerigars (*melopsittacus undulatus*): I. Contact calls," J. Comp. Psychol. 102, 236-247.

Cristie, P. J., Mennill, D. J., and Ratcliffe, L. M. (**2004**). "Pitch shifts and song structure indicate male quality in the dawn chorus of black-capped chickadees," Behav Ecol Sociobiol 55, 341-348.

Cynx, J. (**1990**). "Experimental-determination of a unit of song production in the zebra finch (*taeniopygia guttata*)," J. Comp. Psychol. 104, 3-10.

Dooling, R. J., Gephart, B. F., Price, P. H., McHale, C., and Brauth, S. E. (**1987**). "Effects of deafening on the contact calls of the budgerigar (*melopsittacus undulatus*)," Anim. Beh. 35, 1264-1266.

Dooling, R. J., Ryals, B. M., and Manabe, K. (**1997**). "Recovery of hearing and vocal behavior after hair-cell regeneration," Proc. Natl. Acad. Sci. USA 94, 14206-14210.

Farabaugh, S., and Dooling, R. J. (**1996**). "Acoustic communication in parrots: Laboratory and field studies of budgerigars, *melopsittacus undulatus*," in *Ecology and evolution of acoustic communication in birds*, edited by D. E. Kroodsma, and E. H. Miller (Cornell University Press, Ithaca, NY), pp. 97-118.

Farabaugh, S. M., Dent, M. L., and Dooling , R. J. (**1998**). "Hearing and vocalizations of wild-caught australian budgerigars *(melopsittacus undulatus)*," Journal of Comparative Psychology 112, 74-81.

Farabaugh, S. M., Linzenbold, A., and Dooling, R. J. (**1994**). "Vocal plasticity in budgerigars (*melopsittacus undulatus*): Evidence for social factors in the learning of contact calls," J. Comp. Psychol. 108, 81-92.

Franz, M., and Goller, F. (**2002**). "Respiratory units of motor production and song imitation in the zebra finch," J Neurobiol 51, 129-141.

Goller, F., Mallinckrodt, M., and Torti, S. D. (**2004**). "Beak gape dynamics during song in the zebra finch," Journal of Neurobiology 59, 289-303.

Heaton, J. T., and Brauth, S. E. (**1999**). "Effects of deafening on the development of nestling and juvenile vocalizations in budgerigars (*melopsittacus undulatus*)," J. Comp. Psychol. 113, 314-320.

Hoese, W. J., Podos, J., Boetticher, N. C., and Nowicki, S. (**2000**). "Vocal tract function in birdsong production: Experimental manipulation of beak movements," J Exp Biol 203 Pt 12, 1845-1855.

Manabe, K., and Dooling, R. J. (**1997**). "Control of vocal production in budgerigars (melopsittacus undulatus): Selective reinforcement, call differentiation, and stimulus control," Behav Process 41, 117-132.

Manabe, K., Dooling, R. J., and Brittan-Powell, E. F. (**2008**). "Vocal learning in budgerigars (*melapsittacus undulatus*): Effects of an acoustic reference on vocal matching," Journal of the Acoustical Society of America 123, 1729-1736.

Manabe, K., Kawashima, T., and Staddon, J. E. R. (**1995**). "Differential vocalization in budgerigars: Towards an experimental analysis of naming," J. Exp. Anal. Behav. 63, 111-126.

Manabe, K., Sadr, E. I., and Dooling, R. J. (**1998**). "Control of vocal intensity in budgerigars (*melopsittacus undulatus*): Differential reinforcement of vocal intensity and the lombard effect," J. Acoust. Soc. Am. 103, 1190-1198.

Manabe, K., Staddon, J. E. R., and Cleaveland, J. M. (**1997**). "Control of vocal repertoire by reward in budgerigars *(melopsittacus undulatus)*," Journal of Comparative Psychology 111, 50-62.

Metzner, W., Zhang, S., and Smotherman, M. (**2002**). "Doppler-shift compensation behavior in horseshoe bats revisited: Auditory feedback controls both a decrease and an increase in call frequency," J Exp Biol 205, 1607-1616.

Osmanski, M. S., and Dooling, R. J. (**2004**). "Measures of acoustic variation in directed budgerigar vocal production," in *Association for Research in Otolaryngology* (Daytona Beach, FL).

Podos, J. (**1996**). "Motor constraints on vocal development in a songbird," Animal Behaviour 51, 1061-1070.

Podos, J. (**1997**). "A performance constraint on the evolution of trilled vocalizations in a songbird family (*passeriformes: Emberizidae*)," Evolution 51, 537-551.

Podos, J. (**2001**). "Correlated evolution of morphology and vocal signal structure in darwin's finches," Nature 409, 185-188.

Podos, J., Southall, J. A., and Rossi-Santos, M. R. (**2004**). "Vocal mechanics in darwin's finches: Correlation of beak gape and song frequency," J Exp Biol 207, 607-619.

Riebel, K., and Todt, D. (**1997**). "Light flash stimulation alters the nightingale's singing style: Implications for song control mechanisms," Behaviour 134, 789-808.

Slabbekoorn, H., and Peet, M. (**2003**). "Birds sing at a higher pitch in urban noise," Nature 424, 267.

Smotherman, M., Zhang, S., and Metzner, W. (**2003**). "A neural basis for auditory feedback control of vocal pitch," J Neurosci 23, 1464-1477.

Tchernichovski, O., Mitra, P. P., Lints, T., and Nottebohm, F. (**2001**). "Dynamics of the vocal imitation process: How a zebra finch learns its song," Science 291, 2564-2569.

Westneat, M. W., Long Jr., J. H., Hoese, W., and Nowicki, S. (**1993**). "Kinematics of birdsong: Functional correlation of cranial movements and acoustic features in sparrows," J Exp Biol 182, 147-171.

Chapter 6 - GENERAL SUMMARY AND DISCUSSION

This dissertation describes a series of behavioral experiments examining how budgerigars learn their contact calls. These experiments show that auditory information alone is not sufficient for learning, that call production is dependent on an auditory feedback system that operates across, rather than within, calls, and that this system has important restrictions, such as learning through piecemeal changes within call segments rather than learning the acoustic pattern of an entire call all at once. Specifically, I was able to answer the following questions:

1. Do budgerigars show vocal learning (broadly defined to include contextual learning) based solely on auditory information? No, birds did not alter their vocal output or change acoustic parameters of their dominant call-type during calling bouts. Birds decreased the average frequency of their non-dominant call, but this decrease did not reflect call convergence between pair members. No other parameters changed in the non-dominant call-type.

2. What is the relative salience of visual versus acoustic stimuli in cueing a vocal response in budgerigars? Budgerigars can easily learn to produce a specific contact call to location differences in both visual and acoustic stimuli and to quality differences in visual stimuli. They did not learn to produce distinct calls to quality differences in auditory stimuli, even if those stimuli were the same ones the bird was required to produce (i.e., the call to be produced was the same as the call presented to the bird). However, performance improved when the same stimuli were presented in a ‘natural’ context of a background of vocalizing birds. These results confirm previous

findings showing a kind of social facilitation in budgerigar vocal learning (e.g., Farabaugh *et al.*, 1994; Brittan-Powell *et al.*, 1997; Manabe *et al.*, 2008).

3. Do budgerigars compensate for changes in the level of auditory feedback? Yes, birds increased the amplitude of their vocalizations in the presence of white noise (Lombard effect) and reduced the level of their vocal output when provided with amplified feedback of their own vocalizations (Fletcher effect). Intensity changes were associated with concomitant changes in contact call frequency and duration, a previously unreported finding in this species (e.g., Manabe *et al.*, 1998), but one that is consistent with findings in the human literature (e.g., Lane and Tranel, 1971; Traunmüller and Eriksson, 2000).

4. Are budgerigars sensitive to the spectral and/or temporal pattern of auditory feedback? Yes, birds produced incomplete and distorted calls throughout a test session when provided with delayed AF, a reversed version of their own call, or another bird's call as feedback. Vocal disruptions included changes to the peak frequency, amplitude, duration and spectrotemporal structure of calls. Under DAF conditions, one delay length (e.g., 25 ms) generated the most vocal errors, with longer delays producing comparatively fewer errors. This parallels work showing a maximally-disruptive delay length in humans.

5. Can budgerigars be driven to alter the pitch of their vocalizations? Yes, but birds did not make changes to the frequency of their contact calls when constrained to keep the spectrotemporal structure of the entire call the same. Instead, they altered the overall average frequency of their calls across multiple sessions by making adjustments to certain call segments relative to others. These changes also

entailed significant, bird-specific adjustments in several acoustic parameters, including 3dB bandwidth and amplitude.

Finally, these results allow us to weigh in on the question of whether budgerigars produce contact calls ballistically. Findings show that calls are not subject to real-time modification and are produced in a ballistic fashion. For example, the auditory feedback effects described in Chapters 3(i.e., Fletcher effect) and 4 (e.g., delayed auditory feedback) did not occur during feedback delivery within a call. Instead, changes were made on subsequent calls, presumably based on feedback from the previous vocalization. This is perhaps because there is not enough time to make within-call changes to a vocalization <200 milliseconds long once it is initiated.

Although individual calls are produced ballistically, however, vocal changes occurring over time are not made at the level of the whole call. Instead, results from Chapters 2 (i.e., non-dominant call changes during calling bouts), 3 (i.e., Lombard and Fletcher effects), and 5 (i.e., changing vocal pitch) show that birds make piecemeal changes to call segments rather than global changes across an entire call. These changes were seen as increases or decreases in certain segments of the frequency (and amplitude) contours of calls compared to other segments. This is consistent with data on call learning and development in budgerigars showing that new calls are formed through the modification of call elements (Farabaugh *et al.*, 1994; Farabaugh and Dooling, 1996; Brittan-Powell *et al.*, 1997; Manabe and Dooling, 1997; Manabe *et al.*, 2008) and suggests that this segmental plasticity is an important part of the call learning process in budgerigars.

Future Directions

These dissertation studies describe mechanisms of vocal control and production in budgerigars and point to some intriguing avenues for future research on call learning in these birds:

- Budgerigars learn calls by making changes to small call segments and not to the entire call, but we do not know how much control they really have over individual call elements or whether some segments are more plastic than others. For example, can they make changes to any portion of a call or only to specific segments? Do particular segments show more plasticity than other segments? Two different experimental methods could be used to answer these kinds of questions. First, we could provide altered auditory feedback only over certain portions of a call to examine whether, and in what ways, targeted bursts of feedback interfere with call production. Similarly, we can test to see whether budgerigars can be trained to selectively modify only certain call segments through differential reinforcement.

- Altering auditory feedback results in changes to vocal output in these birds. However, we do not know whether altered feedback of one call affects another, different call. For example, does increasing the feedback intensity (i.e., Fletcher effect) of one call result in decreasing vocal loudness of both call-types? This question points to the potential neural mechanisms underlying call production. For example, feedback effects that transfer between two different call-types would suggest that there is a common feedback mechanism that monitors production of all calls rather than a series of more localized, call-specific feedback mechanisms. To answer this question, we can train birds to produce two different calls to each of two

LEDs (as in the experiments described in Chapter 2) but only provide altered feedback during production of one call. The bird would receive normal call feedback during production of the other call.

- Finally, we could use these operant techniques to examine the control of vocal behavior in songbirds. This would allow for behavioral investigations using stricter methods than previous songbird work has accomplished and would potentially offer new insights and novel ways of examining song learning using both behavioral and neurophysiological techniques. It may be fruitful to try a number of species, included age-limited learners (e.g., zebra finches), seasonal learners (e.g., canaries), and lifetime learners (e.g., starlings) to maximize comparisons between groups. This would provide a rigorous comparative framework that can be compared to work in humans and in which we can better understand the mechanisms underlying how learned vocal repertoires are acquired and maintained in a number of different species.

References

Brittan-Powell, E. F., Dooling, R. J., and Farabaugh, S. M. (**1997**). "Vocal development in budgerigars (*Melopsittacus undulatus*): contact calls," J. Comp. Psychol. **111**, 226-241.

Farabaugh, S., and Dooling, R. J. (**1996**). "Acoustic communication in parrots: Laboratory and field studies of budgerigars, *Melopsittacus undulatus*," in *Ecology and Evolution of Acoustic Communication in Birds*, edited by D. E. Kroodsma, and E. H. Miller (Cornell University Press, Ithaca, NY), pp. 97-118.

Farabaugh, S. M., Linzenbold, A., and Dooling, R. J. (**1994**). "Vocal plasticity in budgerigars (*Melopsittacus undulatus*): evidence for social factors in the learning of contact calls," J. Comp. Psychol. **108**, 81-92.

Lane, H., and Tranel, B. (**1971**). "Lombard Sign and Role of Hearing in Speech," Journal of Speech and Hearing Research **14**, 677-709.

Manabe, K., and Dooling, R. J. (**1997**). "Control of vocal production in budgerigars (Melopsittacus undulatus): Selective reinforcement, call differentiation, and stimulus control," Behav Process **41**, 117-132.

Manabe, K., Dooling, R. J., and Brittan-Powell, E. F. (**2008**). "Vocal learning in Budgerigars (*Melapsittacus undulatus*): Effects of an acoustic reference on vocal matching," Journal of the Acoustical Society of America **123**, 1729-1736.

Manabe, K., Sadr, E. I., and Dooling, R. J. (**1998**). "Control of vocal intensity in budgerigars (*Melopsittacus undulatus*): Differential reinforcement of vocal intensity and the Lombard effect," J. Acoust. Soc. Am. **103**, 1190-1198.

Traunmüller, H., and Eriksson, E. (**2000**). "Acoustic effects of variation in vocal effort by men, women, and children," Journal of the Acoustical Society of America **107**, 3438-3451.

Bibliography

Ali, N. J., Farabaugh, S., and Dooling, R. (**1993**). "Recognition of contact calls by the budgerigar (*melopsittacus undulatus*)," B Psychonomic Soc 31, 468-470.

Banta Lavenex, P. (**2000**). "Lesions in the budgerigar vocal control nucleus nlc affect production, but not memory, of english words and natural vocalizations," Journal of Comparative Neurology 421, 437-460.

Baptista, L. F., and Gaunt, L. L. (**1997**). "Interaction and vocal development in birds," in *Social influences on vocal development*, edited by C. T. Snowdon, and M. Hausberger (Cambridge University Press, Cambridge, England), pp. 23-40.

Baptista, L. F., and Petrinovich, L. (**1984**). "Social interaction, sensitive phases and the song template hypothesis in the white-crowned sparrow," Animal Behav. 32, 172-181.

Baptista, L. F., and Schuchmann, K. L. (**1990**). "Song learning in the anna hummingbird (*calyptae anna*)," Ethology 84, 15-26.

Bauer, J. J., Mittal, J., Larson, C. R., and Hain, T. C. (**2006**). "Vocal responses to unanticipated perturbations in voice loudness feedback: An automatic mechanism for stabilizing voice amplitude," Journal of the Acoustical Society of America 119, 2363-2371.

Beecher, M. D., Stoddard, P. K., Campbell, S. E., and Horning, C. L. (**1996**). "Repertoire matching between neighbouring song sparrows," Animal Behaviour 51, 917-923.

Bloodstein, O. (**1995**). *A handbook on stuttering* (National Easter Seal Society, Chicago, IL).

Bolles, R. C. (**1973**). "The comparative psychology of learning: The selective association principle and some problems with 'general' laws of learning," in *Perspectives in animal behavior*, edited by G. Bermant (Scott, Foresman and Co., Glenview, IL).

Borden, G. J. (**1979**). "An interpretation of research of feedback interruption in speech," Brain Lang 7, 307-319.

Bottjer, S. W. (**2004**). "Developmental regulation of basal ganglia circuitry during the sensitive period for vocal learning in songbirds," in *Behavioral neurobiology of birdsong*, edited by H. P. Zeigler, and P. Marler (New York Academy of Sciences, New York), pp. 395-415.

Boughman, J. W. (**1998**). "Vocal learning by greater spear-nosed bats," Proceedings of the Royal Society of London B 265, 227-233.

Boughman, J. W., and Moss, C. F. (**2003**). "Social sounds: Vocal learning and development of mammal and bird calls," in *Acoustic communication, springer handbook of auditory research*, edited by A. M. Simmons, A. N. Popper, and R. R. Fay (Springer-Verlag, New York), pp. 138-224.

Bowe, C. A., Miller, J. D., and Green, L. (**1987**). "Qualities and locations of stimuli and responses affecting discrimination learning of chinchillas (chinchilla laniger) and pigeons *(columba livia)*," Journal of Comparative Psychology 101, 132-138.

Brainard, M. S. (**2004**). "Contributions of the anterior forebrain pathway to vocal plasticity," in *Behavioral neurobiology of birdsong*, edited by H. P. Zeigler, and P. Marler (New York Academy of Sciences, New York), pp. 377-394.

Brainard, M. S., and Doupe, A. J. (**2000**). "Auditory feedback in learning and maintenance of vocal behaviour," Nature Reviews. Neuroscience 1, 31-40.

Brauth, S., Liang, W., Roberts, T. F., Scott, L. L., and Quinlan, E. M. (**2002**). "Contact call-driven zenk protein induction and habituation in telencephalic auditory pathways in the budgerigar (melopsittacus undulatus): Implications for understanding vocal learning processes," Learn Mem 9, 76-88.

Brauth, S. E., Heaton, J. T., Durand, S. E., Liang, W., and Hall, W. S. (**1994**). "Functional anatomy of forebrain auditory pathways in the budgerigar (melopsittacus undulatus)," Brain, Behavior And Evolution 44, 210-233.

Brauth, S. E., Heaton, J. T., Shea, S. D., Durand, S. E., and Hall, W. S. (**1997**). "Functional anatomy of forebrain vocal control pathways in the budgerigar (*Melopsittacus undulatus*),"Proc. NY Acad. Sci., 807, 368-385.

Brenowitz, E. A., and Beecher, M. D. (**2005**). "Song learning in birds: Diversity and plasticity, opportunities and challenges," Trends Neurosci 28, 127-132.

Brittan-Powell, E. F., Dooling, R. J., and Farabaugh, S. M. (**1997**). "Vocal development in budgerigars (*melopsittacus undulatus*): Contact calls," J. Comp. Psychol. 111, 226-241.

Brittan-Powell, E. F., Dooling, R. J., Larsen, O. N., and Heaton, J. T. (**1997**). "Mechanisms of vocal production in budgerigars (melopsittacus undulatus)," The Journal Of The Acoustical Society Of America 101, 578-589.

Brockway, B. F. (**1964a**). "Ethological studies of the budgerigar (*melopsittacus undulatus*): Non-reproductive behavior," Behavior 22, 193-222.

Brockway, B. F. (**1964b**). "Ethological studies of the budgerigar (*melopsittacus undulatus*): Reproductive behavior," Behavior 23, 294-324.

Brockway, B. F. (**1969**). "Roles of budgerigar vocalization in the integration of breeding behavior," in *Bird vocalizations*, edited by R. A. Hinde (Cambridge University Press, London), pp. 131-158.

Brown, S. D., and Dooling, R. J. (**1992**). "Perception of conspecific faces by budgerigars (*melopsittacus undulatus*): I. Natural faces," J. Comp. Psychol. 106, 203-216.

Brown, S. D., and Dooling, R. J. (**1993**). "Perception of conspecific faces by budgerigars (*melopsittacus undulatus*): Ii. Synthetic models," J. Comp. Psychol. 107, 48-60.

Brown, S. D., Dooling, R. J., and O'Grady, K. (**1988**). "Perceptual organization of acoustic stimuli by budgerigars (*melopsittacus undulatus*): Iii. Contact calls," J. Comp. Psychol. 102, 236-247.

Brumm, H., and Todt, D. (**2002**). "Noise-dependent song amplitude regulation in a territorial songbird.," Anim. Behav. 63, 891-897.

Burdick, C. K. (**1979**). "The effect of behavioral paradigm on auditory discrimination learning: A literature review," Journal of Audiology Research 19, 59-82.

Burnett, T. A., Freedland, M. B., Larson, C. R., and Hain, T. C. (**1998**). "Voice f0 responses to manipulations in pitch feedback," J. Acoust. Soc. Am. 103, 3153-3161.

Chase, R. (**1965**). "An information-flow model of the organization of motor activity i: Transduction, transmission, and central control of sensory information," Journal of Nervous and Mental Disorders 140, 239-251.

Clayton, D. F. (**2004**). "Songbird genomics : Methods, mechanisms, opportunities, and pitfalls," in *Behavioral neurobiology of birdsong*, edited by H. P. Zeigler, and P. Marler (New York Academy of Sciences, New York), pp. 45-60.

Cristie, P. J., Mennill, D. J., and Ratcliffe, L. M. (**2004**). "Pitch shifts and song structure indicate male quality in the dawn chorus of black-capped chickadees," Behav Ecol Sociobiol 55, 341-348.

Cunningham, M. A., and Baker, M. C. (**1983**). "Vocal learning in white-crowned sparrows: Sensitive phases and song dialects," Behav Ecol Sociobiol 13, 259-269.

Cynx, J. (**1990**). "Experimental-determination of a unit of song production in the zebra finch (*taeniopygia guttata*)," J. Comp. Psychol. 104, 3-10.

Cynx, J., Lewis, R., Tavel, B., and Tse, H. (**1998**). "Amplitude regulation of vocalizations in noise by a songbird, taeniopygia guttata," Animal Behav. 56, 107-113.

Cynx, J., and Von Rad, U. (**2001**). "Immediate and transitory effects of delayed auditory feedback on bird song production," Anim. Behav. 62, 305-312.

Dave, A. S., and Margoliash, D. (**2000**). "Song replay during sleep and computational rules for sensorimotor vocal learning," Science 290, 812-816.

Dent, M. L. and Dooling, R. J. (**2003a**). "Investigations of the precedence effect in budgerigars: Effects of stimulus type, intensity, duration, and location," J. Acoust. Soc. Am., 113(4), 2146-2158.

Dent, M. L. and Dooling, R. J. (**2003b**). "Investigations of the precedence effect in budgerigars: The perceived location of auditory images," J. Acoust. Soc. Am., 113(4), 2159-2169.

Dent, M. L. and Dooling, R. J. (**2004**). "The precedence effect in three species of birds (*Melopsittacus undulatus, Serinus canaria*, and *Taeniopygia guttata*)," J. Comp. Psychol., 118(3), 325-331

Deregnaucourt, S., Mitra, P. P., Feher, O., Maul, K. K., Lints, T. J., and Tchernichovski, O. (**2004**). "Song development: In search of the error signal," in *Behavioral neurobiology of birdsong*, edited by H. P. Zeigler, and P. Marler (New York Academy of Sciences, New York), pp. 364-376.

Dobrzecka, C., Szwejkowska, G., and Konorski, J. (**1966**). "Qualitative versus directional cues in two forms of differentiation," Science 153, 87-89.

Dooling, R. J., Brown, S. D., Park, T. J., and Okanoya, K. (**1990**). "Natural perceptual categories for vocal signals in budgerigars (*melopsittacus undulatus*)," in *Comparative perception*, edited by W. C. Stebbins, and M. A. Berkley (John Wiley & Sons, New York), pp. 345-373.

Dooling, R. J., Gephart, B. F., Price, P. H., McHale, C., and Brauth, S. E. (**1987**). "Effects of deafening on the contact calls of the budgerigar (*melopsittacus undulatus*)," Anim. Beh. 35, 1264-1266.

Dooling, R. J., Ryals, B. M., and Manabe, K. (**1997**). "Recovery of hearing and vocal behavior after hair-cell regeneration," Proc. Natl. Acad. Sci. USA 94, 14206-14210.

Dooling, R. and Searcy, M. (**1980**). "Early perceptual selectivity in the swamp sparrow," Dev. Psychobiol. 13, 499-506.

Doupe, A. J., and Kuhl, P. K. (**1999**). "Birdsong and human speech: Common themes and mechanisms," Annu. Rev. Neurosci. 22, 567-631.

Draegert, G. L. (**1951**). "Relationships between voice variables and speech intelligibility in high level noise," Speech Monographs 18, 272-278.

Dreher, J. J., and O'Neill, J. J. (**1958**). "Effects of ambient noise on speaker intelligibility of words and phrases," Laryngoscope 68, 539-548.

Durand, S. E., Heaton, J. T., Amateau, S. K., and Brauth, S. E. (**1997**). "Vocal control pathways through the anterior forebrain of a parrot (melopsittacus undulatus)," The Journal Of Comparative Neurology 377, 179-206.

Eliades, S. J. and Wang, X. (**2008**). "Neural substrates of vocalization feedback monitoring in primate auditory cortex," Nature, Advance online publicaton May 4, 2008.

Elman, J. L. (**1981**). "Effects of frequency-shifted feedback on the pitch of vocal productions," J. Acoust. Soc. Am. 70, 45-50.

Fairbanks, G. (**1954**). "Systematic research in experimental phonetics i: A theory of the speech mechanism as a servosystem," Journal of Speech & Hearing Disorders 19, 133-139.

Fairbanks, G. (**1955**). "Selective vocal effects of delayed auditory feedback," Journal of Speech & Hearing Disorders 20, 333-346.

Falls, J. B. (**1992**). "Playbacks: A historical perspective," in *Playback and studies of animal communication*, edited by P. K. McGregor (Plenum Press, New York), pp. 11-33.

Farabaugh, S., and Dooling, R. J. (**1996**). "Acoustic communication in parrots: Laboratory and field studies of budgerigars, *melopsittacus undulatus*," in *Ecology and evolution of acoustic communication in birds*, edited by D. E. Kroodsma, and E. H. Miller (Cornell University Press, Ithaca, NY), pp. 97-118.

Farabaugh, S. M., Brown, E. D., and Dooling, R. J. (**1992**). "Analysis of warble song of the budgerigar, melopsittacus undulatus," Bioacoustics 4, 111-130.

Farabaugh, S. M., Dent, M. L., and Dooling, R. J. (**1998**). "Hearing and vocalizations in native australian budgerigars (melopsittacus undulatus)," J. Comp. Psychol. 112, 74-81.

Farabaugh, S. M., Linzenbold, A., and Dooling, R. J. (**1994**). "Vocal plasticity in budgerigars (*melopsittacus undulatus*): Evidence for social factors in the learning of contact calls," J. Comp. Psychol. 108, 81-92.

Finney, S. A., and Warren, W. H. (**2002**). "Delayed auditory feedback and rhythmic tapping: Evidence for a critical interval shift," Perception & Psychophysics 64, 896-908.

Fletcher, N. H., and Tarnopolsky, A. (**1999**). "Acoustics of the avian vocal tract," Journal of the Acoustical Society of America 105, 35-49.

Franz, M., and Goller, F. (**2002**). "Respiratory units of motor production and song imitation in the zebra finch," J Neurobiol 51, 129-141.

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," J Comp Neurol 426, 182-196.

Garcia, J., Hankins, W. G., and Rusiniak, K. W. (**1974**). "Behavioral regulation of the milieu interne in man and rat," Science 185, 824-831.

Gerhardt, H. C. (**1994**). "The evolution of vocalization in frogs and toads," Annual Review of Ecology and Systematics 25.

Glaze, C. M., and Troyer, T. W. (**2006**). "Temporal structure in zebra finch song: Implications for motor coding," Journal of Neuroscience 26, 991-1005.

Goller, F., Mallinckrodt, M., and Torti, S. D. (**2004**). "Beak gape dynamics during song in the zebra finch," Journal of Neurobiology 59, 289-303.

Greenberg, S. (**1999**). "Speaking in shorthand: A syllable-centric perspective for understanding pronunciation variation," Speech Commun 29.

Guenther, F. H. (**2001**). "Neural modeling of speech production," in *Speech motor control in normal and disordered speech*, edited by B. Maassen, W. Hulstijn, R. Kent, H. F. M. Peters, and P. H. M. M. van Lieshout (Nijmegen, Uttgeverij Vantilt), pp. 12-15.

Guenther, F. H. (**2006**). "Cortical interactions underlying the production of speech sounds," Journal of Communication Disorders, 39, 350-365.

Gyger, M., Marler, P., and Pickert, R. (**1987**). "Semantics of an avian alarm call system - the male domestic-fowl, gallus-domesticus," Behav. 102, 15-40.

Hall, W. S., Brauth, S. E., and Heaton, J. T. (**1994**). "Comparison of the effects of lesions in nucleus basalis and field 'l' on vocal learning and performance in the budgerigar (melopsittacus undulatus)," Brain, Behavior And Evolution 44, 133-148.

Hanley, T. D., and Steer, M. D. (**1949**). "Effect of level of distracting noise upon speaking rate, duration and intensity," Journal of Speech & Hearing Disorders 14, 363-368.

Hashimoto, Y. and Sakai, K. (**2003**). "Brain activations during conscious self-monitoring of speech production with delayed auditory feedback: An fMRI study," Human Brain Mapping, 20, 22-28.

Hausberger, M. (**1997**). "Social influences on song acquisition and sharing in the european starling *(sturnus vulgaris*)," in *Social influences on vocal development*, edited by C. T. Snowdon, and M. Hausberger (Cambridge University Press, Cambridge, England), pp. 128-156.

Heaton, J. T., and Brauth, S. E. (**1999**). "Effects of deafening on the development of nestling and juvenile vocalizations in budgerigars (*melopsittacus undulatus*)," J. Comp. Psychol. 113, 314-320.

Heaton, J. T., and Brauth, S. E. (**2000**). "Effects of lesions of the central nucleus of the anterior archistriatum on contact call and warble song production in the budgerigar (melopsittacus undulatus)," Neurobiol Learn Mem 73, 207-242.

Heaton, J. T., Dooling, R. J., and Farabaugh, S. M. (**1999**). "Effects of deafening on the calls and warble song of adult budgerigars (*melopsittacus undulatus*)," J. Acoust. Soc. Am. 105, 2010-2019.

Heaton, J. T., Farabaugh, S. M., and Brauth, S. E. (**1995**). "Effect of syringeal denervation in the budgerigar (melopsittacus undulatus): The role of the syrinx in call production," Neurobiology of Learning and Memory 64, 68-82.

Heinks-Maldonado, T. H., and Houde, J. F. (**2005**). "Compensatory responses to brief perturbations of speech amplitude," Acoustics Research Letters Online 6, 131-137.

Hile, A. G., Plummer, T. K., and Striedter, G. F. (**2000**). "Male vocal imitation produces call convergence during pair bonding in budgerigars, *melopsittacus undulatus*," Anim. Behav. 59, 1209-1218.

Hile, A. G., and Striedter, G. F. (**2000**). "Call convergence within groups of female budgerigars (*melopsittacus undulatus*)," Ethol. 106, 1105-1114.

Hinde, R. A., and Hinde, J. (eds). (**1973**). *Constraints on learning: Limitations and predispositions* (Academic Press, New York).

Hoese, W. J., Podos, J., Boetticher, N. C., and Nowicki, S. (**2000**). "Vocal tract function in birdsong production: Experimental manipulation of beak movements," J Exp Biol 203 Pt 12, 1845-1855.

Houde, J. F., Nagarajan, S. S., Sekihara, K., and Merzenich, M. M. (**2002**). "Modulation of the auditory cortex during speech: An MEG study," Journal of Cognitive Neuroscience, 14, 1125-1138.

Hough, G. E., and Volman, S. F. (**2002**). "Short-term and long-term effects of vocal distortion on song maintenance in zebra finches," Journal of Neuroscience 22, 1177-1186.

Howell, P. (**2002**). "The explan theory of fluency control applied to the treatment of stuttering by altered feedback and operant procedures," in *Current issues in linguistic theory: Pathology and therapy of speech disorders*, edited by E. Fava (John Benjamins, Amsterdam), pp. 95-118.

Howell, P., and Archer, A. (**1984**). "Susceptibility to the effects of delayed auditory feedback," Percept. & Psychophys. 36, 296-302.

Howell, P., and Sackin, S. (**2002**). "Timing interference to speech in altered listening conditions," Journal of the Acoustical Society of America 111, 2842-2852.

Hughes, M. S., Nowicki, S., and Lohr, B. (**1998**). "Call learning in black-capped chickadees (*parus atricapillus*): The role of experience in the development of 'chick-a-dee' calls," Ethology 104, 232-249.

Janik, V. M., and Slater, P. J. B. (**1997**). "Vocal learning in mammals," in *Advances in the study of behaviour*, edited by P. J. B. Slater, J. S. Rosenblatt, C. T. Snowdon, and H. Milinski (Academic Press, New York), pp. 59-99.

Janik, V. M., and Slater, P. J. B. (**2000**). "The different roles of social learning in vocal communication," Animal Behavior 60, 1-11.

Jarvis, E. D. (**2004**). "Learned birdsong and the neurobiology of human language," Ann Ny Acad Sci 1016.

Jarvis, E. D. (**2006**). "Selection for and against vocal learning in birds and mammals," Ornithol Sci 5, 5-14.

Jarvis, E. D., and Mello, C. V. (**2000**). "Molecular mapping of brain areas involved in parrot vocal communication," The Journal Of Comparative Neurology 419, 1-31.

Jones, G., and Ransome, R. D. (**1993**). "Echolocation calls of bats are influenced by maternal effects and change over a lifetime," Proceedings of the Royal Society of London B 252, 125-128.

Jürgens, U. (**1992**). "On the neurobiology of vocal communication," in *Nonverbal vocal communication*, edited by H. Papousek, U. Jürgens, and M. Papousek (Cambridge University Press, Paris), pp. 31-42.

Jürgens, U. (**1995**). "Neuronal control of vocal production in non-human and human primates," in *Current topics in primate vocal communication*, edited by E. Zimmerman, J. D. Newman, and U. Jürgens (Plenum Press, New York), pp. 199-206.

Jürgens, U. (**2002**). "Neural pathways underlying vocal control," Neurosci Biobehav R 26, 235-258.

Kobayashi, K. I., and Okanoya, K. (**2003**). "Context-dependent song amplitude control in bengalese finches," Neuroreport 14, 521-524.

Konishi, M. (**1963**). "The role of auditory feedback in the vocal behavior of the domestic fowl," Zeitschrift für Tierpsychologie 20, 349-367.

Konishi, M. (**1965a**). "Effects of deafening on song development in american robins and black-headed grosbeaks," Z Tierpsychol 22, 584-599.

Konishi, M. (**1965b**). "The role of auditory feedback in the control of vocalization in the white-crowned sparrow," Z Tierpsychol 22, 770-783.

Konishi, M. (**2004**). "The role of auditory feedback in birdsong," in *Behavioral neurobiology of birdsong*, edited by H. P. Zeigler, and P. Maler (New York Academy of Sciences, New York), pp. 463-475.

Kroodsma, D. E., and Konishi, M. (**1991**). "A suboscine bird (eastern phoebe, sayornis-phoebe) develops normal song without auditory-feedback," Animal Behav. 42, 477-487.

Kroodsma, D. E., and Miller, E. H. (**1982**). *Acoustic communication in birds* (Academic Press, New York, NY).

Lane, H., and Tranel, B. (**1971**). "Lombard sign and role of hearing in speech," Journal of Speech and Hearing Research 14, 677-709.

Larsen, O. N., and Goller, F. (**1999**). "Role of syringeal vibrations in bird vocalizations," P Roy Soc Lond B Bio 266, 1609-1615.

Larsen, O. N., and Goller, F. (**2002**). "Direct observation of syringeal muscle functions in songbirds and a parrot," J Exp Biol 205, 25-35.

Lashley, K. S. (**1967**). "The problem of serial order in behavior," in *Cerebral mechanisms in behavior*, edited by L. A. Jeffress (Hafner, New York), pp. 112-146.

Lawicka, W. (**1968**). "Differring effectiveness of auditory quality and location cues in two forms of differentiation learning," Acta Biologiae Experimentalis 29, 83-92.

Lee, B. S. (**1950**). "Effects of delayed speech feedback," Journal of the Acoustical Society of America 22, 824-826.

Leonardo, A., and Konishi, M. (**1999**). "Decrystallization of adult birdsong by perturbation of auditory feedback," Nature 399, 466-470.

Lieberman, P. (**2002**). "On the nature and evolution of the neural bases of human language," Am J Phys Anthropol 45, 36-62.

Lombard, E. (**1911**). "Le signe de l'élévation de la voix," Ann. Maladies Oreille, Larynx, Nez, Pharynx 37, 101-119.

Lombardino, A. J., and Nottebohm, F. (**2000**). "Age at deafening affects the stability of learned song in adult male zebra finches," Journal of Neuroscience 20, 5054-5064.

Mammen, D. L., and Nowicki, S. (**1981**). "Individual-differences and within-flock convergence in chickadee calls," Behav Ecol Sociobiol 9, 179-186.

Manabe, K., Cleaveland, M. J., and Staddon, J. E. R. (**1997**). "Control of vocal repertoire by reward in budgerigars (*melopsittacus undulatus*)," J. Comp. Psychol. 111, 50-62.

Manabe, K., and Dooling, R. J. (**1997**). "Control of vocal production in budgerigars (melopsittacus undulatus): Selective reinforcement, call differentiation, and stimulus control," Behav Process 41, 117-132.

Manabe, K., Dooling, R. J., and Brittan-Powell, E. F. (**2008**). "Vocal learning in budgerigars (*melapsittacus undulatus*): Effects of an acoustic reference on vocal matching," Journal of the Acoustical Society of America 123, 1729-1736.

Manabe, K., Kawashima, T., and Staddon, J. E. R. (**1995**). "Differential vocalization in budgerigars: Towards an experimental analysis of naming," J. Exp. Anal. Behav. 63, 111-126.

Manabe, K., Sadr, E. I., and Dooling, R. J. (**1998**). "Control of vocal intensity in budgerigars (*melopsittacus undulatus*): Differential reinforcement of vocal intensity and the lombard effect," J. Acoust. Soc. Am. 103, 1190-1198.

Manabe, K., Staddon, J. E. R., and Cleaveland, J. M. (**1997**). "Control of vocal repertoire by reward in budgerigars *(melopsittacus undulatus)*," Journal of Comparative Psychology 111, 50-62.

Margoliash, D. (**2002**). "Evaluating theories of bird song learning: Implications for future directions," J. Comp. Physiol. A 188, 851-866.

Marler, P. (**1970**). "A comparative approach to vocal learning - song development in white-crowned sparrows," J Comp Physiol Psych 71, 1-&.

Marler, P. (**1981**). "Birdsong: The acquisition of a learned motor skill," Trends In Neurosciences 4, 88-94.

Marler, P. (**2004**). "Bird calls: Their potential for behavioral neurobiology," in *Behavioral neurobiology of birdsong*, edited by H. P. Zeigler, and P. Marler (Annals of the New York Acedemay of Sciences, New York), pp. 31-44.

Marler, P. R., Dooling, R. J. and Zoloth, S. (**1980**). "Comparative perspecitves on ethology and behavioral development," in *Comparative methods in psychology*, edited by M. H. Bornstein (Lawrence Erlbaum Associates, New Jersey), pp. 189-230.

Marler, P., and Peters, S. (**1977**). "Selective vocal learning in a sparrow," Science 198, 519-521.

Mello, C. V. (**2002**). "Mapping vocal communication pathways in birds with inducible gene expression," J Comp Physiol A Neuroethol Sens Neural Behav Physiol 188, 943-959.

Menzel, R. (**1985**). "Learning in honeybee in an ecological and behavioural context," in *Experimental & behavioural ecology*, edited by M. Lindauer and B. Hölldobler (Stuttgart: Fischer), pp. 195-205.

Metzner, W., Zhang, S., and Smotherman, M. (**2002**). "Doppler-shift compensation behavior in horseshoe bats revisited: Auditory feedback controls both a decrease and an increase in call frequency," J Exp Biol 205, 1607-1616.

Miller, C. T., Flusberg, S., and Hauser, M. D. (**2003**). "Interruptibility of long call production in tamarins: Implications for vocal control," J Exp Biol 206, 2629-2639.

Miller, C. T., and Wang, X. (**2006**). "Sensory-motor interaction modulates a primate vocal behavior: Antiphonal calling in common marmosets," Journal of comparative physiology A 192, 27-38.

Miller, J. D., and Bowe, C. A. (**1982**). "Roles of the qualities and locations of stimuli and responses in simple associative learning: The quality-location hypothesis," Pavlovian Journal of Biological Science 17, 129-139.

Mooney, R. (**2004**). "Synaptic mechanisms for auditory-vocal integration and the correction of vocal errors," Ann Ny Acad Sci 1016, 476-494.

Moravec, M. L., Striedter, G. F., and Burley, N. T. (**2006**). "Assortative pairing based on contact call similarity in budgerigars, melopsittacus undulatus," Ethology 112, 1108-1116.

Naguib, M. (**1999**). "Effects of song overlapping and alternating on nocturnally singing nightingales," Animal Behaviour 58, 1061-1067.

Naguib, M., Fichtel, C., and Todt, D. (**1999**). "Nightingales respond more strongly to vocal leaders of simulated dyadic interactions," Proceedings of the Royal Society of London B 266, 537-542.

Neilson, M. D., and Neilson, P. D. (**1991**). "Adaptive model theory of speech motor control and stuttering," in *Speech motor control and stuttering*, edited by H. G. M. Peters, W. Hulstijn, and C. W. Starkweather (Elsevier, Amsterdam), pp. 149-156.

Nelson, D. A. (**1997**). "Social interaction and sensitive phases for song learning: A critical review," in *Social influences on vocal development*, edited by C. T. Snowdon, and M. Hausberger (Cambridge University Press, Cambridge, England), pp. 7-22.

Nelson, D. A., and Marler, P. (**1993**). "Innate recognition of song in white-crowned sparrows - a role in selective vocal learning," Animal Behav. 46, 806-808.

Nordeen, K., and Nordeen, E. (**1992**). "Auditory feedback is necessary for the maintenance of stereotyped song in adult zebra finches," Behavior. Neural. Biol. 57, 58-66.

Nordeen, K. W., and Nordeen, E. J. (**2004**). "Synaptic and molecular mechanisms regulating plasticity during early learning," in *Behavioral neurobiology of* *birdsong*, edited by H. P. Zeigler, and P. Marler (New York Academy of Sciences, New York), pp. 416-437.

Nottebohm, F. (**1972**). "Origins of vocal learning," Am Nat 106, 116-140.

Nottebohm, F. (**1999**). "The anatomy and timing of vocal learning in birds," in *The design of animal communication*, edited by M. D. Hauser, and M. Konishi (MIT Press, Cambridge, MA), pp. 63-110.

Nottebohm, F., and Nottebohm, M. E. (**1971**). "Vocalizations and breeding behav. Of surgically deafened ring doves (streptopelia risoria)," Anim Behav 19, 313-327.

Nottebohm, F., Stokes, T. M., and Leonard, C. M. (**1976**). "Central control of song in the canary, serinus canarius," J Comp Neurol 165, 457-486.

Okanoya, K., and Dooling, R. J. (**1991**). "Perception of distance calls by budgerigars (melopsittacus-undulatus) and zebra finches (poephila-guttata) - assessing species-specific advantages," J. Comp. Psychol. 105, 60-72.

Okanoya, K., and Yamaguchi, A. (**1997**). "Adult bengalese finches (*lonchura striata* var. Domestica) require real-time auditory feedback to produce normal song syntax," J. Neurobiol. 33, 343-356.

Osmanski, M. S., and Dooling, R. J. (**2004**). "Measures of acoustic variation in directed budgerigar vocal production," in *Association for Research in Otolaryngology* (Daytona Beach, FL).

Owings, D. H., and Leger, D. W. (**1980**). "Chatter vocalizations of california ground squirrels: Predator- and social-role specificity," Zeitschrift für Tierpsychologie 46.

Owings, D. H., and Virgina, R. A. (**1978**). "Alarm calls of california ground squirrels *(spermophilus beecheyi)*," Zeitschrift für Tierpsychologie 54.

Park, T. J., and Dooling, R. J. (**1991**). "Sound localization in small birds: Absolute localization in azimuth," J. Comp. Psychol. 105, 125-133.

Payne, R. B. (**1981**). "Song learning and social interaction in indigo buntings," Animal Behavior 29, 688-697.

Pepperberg, I. M. (**1993**). "A review of the effects of social interaction on vocal learning in african grey parrots *(psittacus erithacus)*," Neth J Zool 43, 104-124.

Plummer, T. K., and Striedter, G. F. (**2002**). "Brain lesions that impair vocal imitation in adult budgerigars," J Neurobiol 53, 413-428.

Podos, J. (**1996**). "Motor constraints on vocal development in a songbird," Animal Behaviour 51, 1061-1070.

Podos, J. (**1997**). "A performance constraint on the evolution of trilled vocalizations in a songbird family (*passeriformes: Emberizidae*)," Evolution 51, 537-551.

Podos, J. (**2001**). "Correlated evolution of morphology and vocal signal structure in darwin's finches," Nature 409, 185-188.

Podos, J., Southall, J. A., and Rossi-Santos, M. R. (**2004**). "Vocal mechanics in darwin's finches: Correlation of beak gape and song frequency," J Exp Biol 207, 607-619.

Popp, J. W. (**1989**). "Temporal aspects of singing interactions among territorial ovenbirds *(seiurus aurocapillus)*," Ethology 82, 127-133.

Potash, L. M. (**1972**). "Noice-induced changes in calls of the japanese quail.," Psychon. Sci. 26, 252-254.

Prather, J. F., Peters, S., Nowicki, S., and Mooney, R. (**2008**). " Precise auditory-vocal mirroring in neurons for learned vocal communication," Nature, 451, 305-310.

Price, P. (**1979**). "Developmental determinants of structure in zebra finch song," J. Comp. Physiol. Psych. 93, 260-277.

Pytte, C. L., Rusch, K. M., and Ficken, M. S. (**2003**). "Regulation of vocal amplitude by the blue-throated hummingbird, *lampornis clemenciae*," Animal Behaviour 66, 703-710.

Richards, D. G., Wolz, J. P., and Herman, L. M. (**1984**). "Vocal mimicry of computer-generated sounds and vocal labeling of objects by a bottlenosed dolphin, tursiops truncatus," J. Comp. Psychol. 98, 10-28.

Riebel, K., and Todt, D. (**1997**). "Light flash stimulation alters the nightingale's singing style: Implications for song control mechanisms," Behaviour 134, 789-808.

Ringel, R. L., and Steer, M. D. (**1963**). "Some effects of tactile and auditory alterations on speech output," Journal of Speech and Hearing Research 6, 369-378.

Romand, R., and Ehret, G. (**1984**). "Development of sound production in normal, isolated, and deafened kittens during the first postnatal months," Developmental Psychobiology 17, 629-649.

Sakata, J. T., and Brainard, M. S. (**2006**). "Real-time contributions of auditory feedback to avian vocal motor control," The Journal Of Neuroscience: The Official Journal Of The Society For Neuroscience 26, 9619-9628.

Seyfarth, R. M., and Cheney, D. L. (**1986**). "Vocal development in vervet monkeys," Animal Behavior 34, 1640-1658.

Seyfarth, R. M., Cheney, D. L., and Marler, P. (**1980**). "Monkey responses to three different alarm calls: Evidence of predator classification and semantic communication," Science 210, 801-803.

Shipley, C., Buchwald, J. S., and Carterette, E. C. (**1988**). "The role of auditory feedback in the vocalizations of cats," Experimental Brain Research 69, 431-438.

Siegel, G. M., and Pick, H. L. (**1974**). "Auditory feedback in the regulation of voice," Journal of the Acoustical Society of America 56, 1618-1624.

Sinnott, J. M., Stebbins, W. C., and Moody, D. B. (**1975**). "Regulation of voice amplitude by the monkey," J. Acoust. Soc. Am. 58, 412-414.

Slabbekoorn, H., and Peet, M. (**2003**). "Birds sing at a higher pitch in urban noise," Nature 424, 267.

Smith, D. G., and Norman, D. O. (**1979**). "Leader-follower' singing in red-winged blackbirds," Condor 81, 83-84.

Smotherman, M., Zhang, S., and Metzner, W. (**2003**). "A neural basis for auditory feedback control of vocal pitch," J Neurosci 23, 1464-1477.

Striedter, G. F. (**1994**). "The vocal control pathways in budgerigars differ from those in songbirds," J Comp Neurol 343, 35-56.

Striedter, G. F., Freibott, L., Hile, A. G., and Burley, N. T. (**2003**). "For whom the male calls: An effect of audience on contact call rate and repertoire in budgerigars, melopsittacus undulatus," Animal Behaviour 65, 875-882.

Summers, W. V., Pisoni, D. B., Bernacki, R. H., Pedlow, R. I., and Stokes, M. A. (**1988**). "Effects of noise on speech production: Acoustic and perceptual analyses," Journal of the Acoustical Society of America 84, 917-928.

Takahasi, M., Ikebuchi, M., and Okanoya, K. (**2005**). "Spatiotemporal properties of visual stimuli for song induction in bengalese finches," Neuroreport 16, 1339-1343.

Talmage-Riggs, G., Winter, P., Ploog, D., and Mayer, W. (**1972**). "Effect of deafening on the vocal behaviour of the squirrel monkey (saimiri sciureus). ," Folia Primatol 17, 404-420.

Tchernichovski, O., Mitra, P. P., Lints, T., and Nottebohm, F. (**2001**). "Dynamics of the vocal imitation process: How a zebra finch learns its song," Science 291, 2564-2569.

Thorpe, W. H. (**1958**). "The learning of song patterns by birds, with especial reference to the song of the chaffinch, *fringilla coelebs*," Ibis 100, 535-570.

Todt, D., and Naguib, M. (**2000**). "Vocal interactions in birds: The use of song as a model in communication," in *Advances of the study of behavior*, edited by P. J. B. Slater, J. S. Rosenblatt, C. T. Snowdon, and T. J. Roper (Academic Press, New York), pp. 247-296.

Traunmüller, H., and Eriksson, E. (**2000**). "Acoustic effects of variation in vocal effort by men, women, and children," Journal of the Acoustical Society of America 107, 3438-3451.

Treisman, M. (**1978**). "Bird song dialects, repertoire size, and kin association," Anim. Behav. 26, 814-817.

Troyer, T. W., and Doupe, A. J. (**2000a**). "An associational model of birdsong sensorimotor learning i. Efference copy and the learning of song syllables," J. Neurophysiol. 84, 1204-1223.

Troyer, T. W., and Doupe, A. J. (**2000b**). "An associational model of birdsong sensorimotor learning ii. Temporal hierarchies and the learning of song sequence," J. Neurophysiol. 84, 1224-1239.

Vicario, D. S. (**2004**). "Using learned calls to study sensory-motor integration in songbirds. ," in *Behavioral neurobiology of birdsong*, edited by H. P. Zeigler, and P. Marler (New York Academy of Sciences, New York), pp. 246-262.

Wanker, R., and Fischer, J. (**2001**). "Intra- and interindividual variation in the contact calls of spectacled parrotlets *(forpus conspicillatus)*," Behaviour 138, 709-726.

West, M. J., and King, A. P. (**1988**). "Female visual displays affect the development of male song in the cowbird," Nature 334, 244-246.

Westneat, M. W., Long Jr., J. H., Hoese, W., and Nowicki, S. (**1993**). "Kinematics of birdsong: Functional correlation of cranial movements and acoustic features in sparrows," J Exp Biol 182, 147-171.

Williams, H. (**2004**). "Birdsong and singing behavior," in *Behavioral neurobiology of birdsong*, edited by H. P. Zeigler, and P. Marler (New York Academy of Sciences, New York), pp. 1-30.

Woolley, S. M. N. (**2004**). "Auditory experience and adult song plasticity," in *Behavioral neurobiology of birdsong*, edited by H. P. Zeigler, and P. Marler (New York Academy of Sciences, New York), pp. 208-221.

Woolley, S. M. N., and Rubel, E. W. (**1997**). "Bengalese finches *lonchura striata* domestica depend upon auditory feedback for the maintenance of adult song," J. Neurosci. 17, 6380-6390.

Wright, T. F. (**1996**). "Regional dialects in the contact call of a parrot," P Roy Soc Lond B Bio 263, 867-872.

Wright, T. F., and Dorin, M. (**2001**). "Pair duets in the yellow-naped amazon (psittaciformes: *Amazona auropalliata*): Responses to playbacks of different dialects," Ethology 107, 111-124.

Wright, T. F., and Wilkinson, G. S. (**2000**). "Population genetic structure and vocal dialects in an amazon parrot," Proceedings of the Royal Society of London B 268, 609-616.

Wyndham, E. (**1980**). "Environment and food of the budgerigar (melopsittacus undulatus)," Australian Journal of Ecology 5, 47-61.

Yates, A. J. (**1963**). "Delayed auditory feedback," Psychol Bull 60, 213-232.

Zann, R. A. (**1990**). "Song and call learning in wild zebra finches in south-east australia," Animal Behavior 40, 818-828.

Zann, R. A. (**1996**). *The zebra finch: A synthesis of field and laboratory studies* (Oxford University Press, New York).

Zuberbühler, K. (**2000**). "Referential labeling in diana monkeys," Animal Behavior 59, 917-927.