UC Riverside UC Riverside Electronic Theses and Dissertations

Title

Assessing Animal Vocal Communication Using the Hyperspace Analog to Language (HAL) Model

Permalink <https://escholarship.org/uc/item/1sm4n21w>

Author Kaufman, Allison B.

Publication Date 2010

Peer reviewed|Thesis/dissertation

THE UNIVERSITY OF CALIFORNIA RIVERSIDE

Assessing Animal Vocal Communication Using the Hyperspace Analog to Language (HAL) Model

A Dissertation submitted in partial satisfaction of the requirements for the degree of

Doctor of Philosophy

in

Neuroscience

by

Allison Beth Kaufman

June 2010

Dissertation Committee: Dr. Curt Burgess, Chairperson Dr. Khaleel Razak Dr. Aaron Seitz

Copyright by Allison Beth Kaufman 2010

The Dissertation of Allison Beth Kaufman is approved:

Committee Chairperson

University of California, Riverside

__

__

__

Acknowledgements

The three studies that make up this dissertation were each collaborative efforts, so first and foremost I would like to thank my collaborators – Erin Colbert-White of the University of Georgia on the Cosmo project, Sean Green of SUNY Buffalo and the Singapore Institute of Management and Aaron Seitz of the University of California, Riverside on the humpback whale project, and Sarah Rotschafer of the University of California, Riverside on the mouse project.

I am grateful so many people who have provided advice and support to me – Mike Adams, Adam Bristol, Allen Butt, Yuchin Chein, Dom Cicchetti, Cary Coburn , Jason Cole, Betty Jean Craig, Zana Devitto, Perla Fabelo, Dorothy Fragasy, Elena Grigorenko, Stan Kuczaj, Monica Lurtz, Lori Marino, Brenda McCowan, Andrea Nolan, Rhea Paul, Ryan Robart, Bob Rosenthal, Lisa Scherff, Sara Sparrow, Bob Sternberg, Mike Trujillo, Indre Viskontas, Jodie Ullman, Suzanne Welcome, and Mark Xitco. I was also supported by the Janet M. Boyce Memorial Scholarship and a Chancellor's Dissertation Fellowship.

A few special people – my parents, Jean and Joe Katz, my sister Cindy and her husband Gili, and my in-laws, Alan and Nadeen Kaufman for all their support. I am particularly grateful to my father-in-law for endless statistics advice and editing. Greg and Voica Armstrong and Mihaela Popescu, who, during the last few months have spent considerable time feeding, caring for, babysitting, entertaining, doing the laundry of, and even bathing various members of my family. I probably could have done it without you guys, but it wouldn't have been pretty!

I would like to thank my committee, Aaron Seitz and Khaleel Razak, for their thoughts and comments on the finished dissertation and for their support along the way.

To Curt, my advisor, who managed to put up with my neuroses for seven years, I really have had a wonderful experience. I look forward to collaborating more in the future.

To Genet – we did it! Thank you for all your support, help, humor, advice, encouragement, time, camaraderie, child-raising tips, pancake and coffee consumption, and Lord knows what else.

And to my boys, James and Jacob – I think the best thing about finishing up is getting to cuddle on the bed and watch The Simpsons in the evening with you two. I can't wait!

To James:

You know me - I wrote 70,169 words in this document and I don't have one I can think of to write here.

ABSTRACT OF THE DISSERTATION

Assessing Animal Vocal Communication Using the Hyperspace Analog to Language (HAL) Model

by

Allison B. Kaufman

Doctor of Philosophy, Graduate Program in Neuroscience University of California, Riverside, June 2010 Dr. Curt Burgess, Chairperson

The Hyperspace Analog to Language (HAL) model is used to measure contextual co-occurrence in human language (Lund & Burgess, 1996). In this dissertation, the HAL model was applied to three nonhuman animal systems; the vocalizations of an African gray parrot, the songs of humpback whales, and the courtship songs of male mice (from both a wild-type population and a genetic model for Fragile X syndrome). In all cases, HAL found evidence of contextual co-occurrence and therefore higher order structure in the communication systems. In the case of the parrot, HAL showed contextual clusters stemming from common phrases in the repertoire, showing these phrases had been arrived at via individual word learning and substitution (as opposed to memorization of each and every phrase as a specific entity). In the humpback whale songs, HAL identified Classes of units that could be combined into patterns specific to individual regions. Changes in these patterns and the usage of the Classes may be additional support for the idea of cultural or geographic clans in these marine mammals. In the mouse song, HAL analysis found different co-occurrence Classes for the wild type and knock out (Fragile X model) mice, and established that although the Fragile X mice appear to be putting together courtship songs with the correct syntax, they may not be doing this using a global co-occurrence schema. Much of this research is preliminary and required subjective judgments, in addition to the creation of new statistical techniques. The judgments made and statistical methods developed were seen as the most reasonable options, however further experimentation is necessary in the case of all three experiments.

Table of Contents

List of Figures

Figure number

Page

CHAPTER 1: INTRODUCTION AND METHODS

BACKGROUND

Defining Language

Much recent research and debate has focused on defining language and examining its components in a comparative framework (Christiansen & Kirby, 2003). In a 2005 paper by Fitch, many of the components of the language debate are laid out, along with a review of what has been – and still needs to be – investigated. He identifies three critical areas – speech, syntax, and semantics – that must be explored in both humans and animals in order to effectively define and understand language. He also emphasizes that the study of language in animals other than primates (such as dolphins and birds) is especially important, as it is indicative of analogous evolution between distantly related species, and may show that the selection of particular traits for language is adaptive in multiple species.

In addition to this is a seeming inability to define the idea of communication among animal researchers in general (Rendall, Owren, & Ryan, 2009; Scott-Phillips, 2010; Soltis, 2009). Research is based on definitions that range from the basic premise that communication is defined as the passage of information (Owings & Morton, 1998; Shannon, 1948) to the more complex idea that communication that contains higher-level cognitive or referential meaning can be called language and equated to human speech (Savage-Rumbaugh, 1993; Zuberbuhler, Cheney, & Seyfarth, 1999). For purposes of this paper, I will use simply "an attempt to pass information" as the criterion for communication.

Recursion in Animals

Recursion has always been an important component in a language acquisition mechanism. In 2002, *Science* published a paper by Noam Chomsky and colleagues detailing their new theory on the "faculty of language" (Hauser, Chomsky, & Fitch, 2002). The paper classified human language into two components: (a) the Faculty of Language in the Narrow sense (FLN), which consists of an internal computational system for recursion, and (b) the Faculty of Language in the Broad sense (FLB), which

consists of the FLN, plus sensory-motor and conceptual-intentional systems. One of the main arguments Hauser et al. make is that the FLN, which is comprised mainly of recursive abilities, is unique to humans and distinguishes human language from that of animals (recursive ability refers to the ability to embed a theoretically infinite number of phrases within sentences, for example, "John said that Mary said the boy was playing"). This idea, that recursion is solely a human ability has been specifically challenged by animal researchers.

Several studies of non-human animals have directly addressed the idea that some species may be able to understand recursive structures. Genter et al. (2006) found the ability to understand recursive structures in the European starling (*Sturnus vulgaris*), and other studies have identified similar abilities in parrots (Pepperberg, 1992). The ability to understand sequential regularities more complex than traditional Finite State Grammars¹ (FSGs) has been demonstrated in pigeons (Herbranson & Shimp, 2008)². Savage-Rumbaugh et al. (1993) showed that a bonobo (*Pan paniscus*) was better able to comprehend recursive structures than a two-year-old child, and it has been demonstrated that bottlenose dolphins (*Tursiops truncates*) can comprehend conjoined sentences, an essential component in recursive construction (Herman, Richards, & Wolz, 1984).

In one of the most cited empirical studies on this topic, tamarins (*Saguinus oedipus*) and college students were tested on their ability to learn both FSGs and PSGs (Fitch & Hauser, 2004). The study, which provided *the same amount* of training on PSG and FSG to both tamarins and undergraduates, is, however, extremely flawed. For example, the investigators failed to determine if the humans in their study were actually using a context-free grammar to identify sentences rather than other plausible pattern recognition techniques (Kochanski, 2005). Recursion beyond one to two levels of embedding is virtually unintelligible to humans (for example, the sentence "The rat that the cat that the dog bit chased ate the cheese"); therefore, it makes little sense to assume that participants in the study specifically identified the

 $\frac{1}{1}$

2

A linear grammatical structure

Recursion was not specifically examined in the Herbranson and Shimp study

recursive pattern in "ba la tu li pa ka" (where ba, la, and tu are A syllables and li, pa, and ka are B syllables), as opposed to a non-recursive pattern such as "ba li la pa tu ka" (Fitch & Hauser, 2004).

Several other teams have remediated flawed methodology in studies such as Fitch and Hauser's, only to be met with opposing results. Perruchet and Rey (2005) believed there could be alternate underlying reasons for the Fitch and Hauser results (e.g., the humans could have counted the number of transitions between the voices vocalizing A syllables and B syllables, or they could have identified phrases as having the same number of A's and B's). The researchers modified the experimental procedure of the original study so that participants were required to use recursive patterning to learn the sentences - and found that the human participants *did not learn*. Fitch and Hauser had used two acoustically different tones as their syllables, so Perruchet and Rey used sequences that were recursive on both syllable and tone and tested for each one separately. Participants chose the tonal patterns as the ones that followed the rule they had learned. Friederici et al (2006) used the same procedure in an fMRI study and claimed to have found different areas of activation in the brain during processing of FSG and PSG. However, when de Vries et al. (2008) altered the procedure to test a more precise set up stimuli, A3A2A1B1B2B3 vs. A3A2A1A4B2B3, A3A2A1B1B3B2 vs. A3A2A1A4B2B3, and A3A2A1B1B2B3 vs. A3A2A1B1B3B2, they found it was much more likely that the subjects had used counting rules, rather than hierarchical rules, to complete the task. Participants scored similarly on the first two conditions (which could be differentiated by counting) and at a chance level on the third (which could only be differentiated by the hierarchical structure). In surveys administered after the experiment, none of the students mentioned learning a hierarchical rule.

Most recently, a study attempting to replicate Fitch and Hauser's results (Hochmann, Azadpour, & Mehler, 2008) showed that subjects could differentiate FSG from PSG; however, they also identified as correct (i.e., as PSG) items with uneven numbers of A's and B's (AAAABBB), which are not part of a PSG. The subset of participants who classified all items correctly reported counting the number of A's and B's – not identifying a hierarchical structure – as their technique (Hochmann et al., 2008).

Additional research in this area deals with statistical regularities in communication streams. An often cited study compares the learning of statistical dependencies by tamarins and human infants (Hauser, Newport, & Aslin, 2001; Hauser, Weiss, & Marcus, 2002; Newport, Hauser, Spaepen, & Aslin, 2004; Saffran et al., 2008). In several of these studies, tamarins have shown evidence of the ability to learn and generalize rule-based grammars and statistical dependencies (Hauser et al., 2001; Hauser, Weiss, et al., 2002; Newport et al., 2004). Even more recently (Hauser & Glynn, 2009), the ability to extract rule-based grammars was shown in free-ranging Japanese macaques (*Macaca fuscata*). This finding expanded the diversity of study subjects to Old World monkeys and to wild animals using artificially arranged patterns of natural vocalizations - rather than captive animals using artificial sounds (Hauser & Glynn, 2009). The research presented in this dissertation is closely linked to the abilities shown by these species to deal with rule based grammars, in addition to parallel abilities found in rats (Toro & Trobalon, 2005). Lastly, Feher et al. (2009) recently demonstrated that song styles in zebra finches (*Taeniopygia guttata*) could develop *de novo*, and, thus, hypothesized that this culture was created from both genetic and environmental components. The environmental component, they further claimed, is subdivided into portions both dependent on the bird's tutor (i.e. culture) and independent of it. When the tutor's song is further broken down into dependent and independent components (with reference to its own tutor), a recursive structure ensues (Fehér, et al., 2009) - which Hauser et al., (2002) claim to be impossible for a non-human species.

Very recent research using a connectionist model known as a Simple Recurrent Network (Elman, 1990) has shown that recursion can be learned via experience; it is not necessary to be innate. Work with this model revealed that it can make novel predictions (which could be confirmed via behavioral testing) about all types of embedding (Christiansen & MacDonald, 2009). This finding is specifically salient because the SRN is a memory model, and one which incorporates memory over time (Elman, 1990). Some of the earliest papers addressing recursive abilities in animals are actually not studies meant to address the idea of recursion, but studies meant to address the idea of memory (Menzel, 1973; Tinklepaugh, 1932). These studies both used experimental procedures that required chimps to remember the location of food (in some cases over an extended amount of time), and only noted tangentially (if at all) that the chimps used

recursive methods to locate and collect their meals. Lastly, studies have shown that the predictive abilities of high dimensional models can be demonstrated using sensorimotor features as input (Howell, Jankowicz, & Becker, 2005), a remarkable way of elucidating the contextual nature of words, that additionally ties full circle to observations of manual recursion in animals (Byrne, Corp, & Byrne, 2001).

Approaches to the Study of Language in Animals

Reznikova (2007) lays out the three basic methodologies that have been used to study language and communication in animals – attempts at direct translation of vocalizations, attempts to teach language to animals, and attempts to quantify characteristics of communication via information theory. The research presented here covers each of these areas, although it is unified by an overarching theme of computational linguistic modeling, which finds its greatest parallels in information theory. Because of the broad and interdisciplinary nature of the approach the present study takes, background from all three perspectives on animal communication research is required.

Direct translation of vocalizations

Reznikova (2007) insightfully points out that researchers have only fully succeeded in decoding two non-human communication systems – the dance of honeybees (von Frisch, 1967) and various types of danger signaling in communally living species such as monkeys and prairie dogs (C.S. Evans & Marler, 1991; Manser, 2001; Seyfarth, Cheney, & Marler, 1980; Slobodchikoff, Kiriazis, Fischer, & Creef, 1991; Zuberbuhler, 2003).

However, researchers have successfully decoded some very important aspects of many animal communication systems. Two abilities – referential communication and combinatorial semantics – are particularly indicative of higher cognitive abilities.

Referential knowledge is the understanding that a signal, which is essentially not a tangible thing, corresponds directly to something that is tangible (for example, an object). While alarm calling is widespread in the animal kingdom (Arnold & Zuberbuhler, 2006a; Griffin, Savani, Hausmanis, &

Lefebvre, 2005; Hollen & Manser, 2006; Hollén & Radford, 2009; Randall, McCowan, Collins, Hooper, & Rogovin, 2005; Randler, 2006; Rendall, et al., 2009; Scott-Phillips, 2010; Seyfarth, et al., 1980; Soltis, 2009; Zuberbühler, Marc, Klaus, Nicola, & Vincent, 2009), semantic referential abilities were first found in Diana monkeys (*Cercopithecus diana diana*). One of the initial experiments involved the desensitization of these monkeys to alarm calls; in this particular species, male and female monkeys possess different alarm calls, and female alarm calls can be elicited by either the vocalization of a predator (eagle or leopard) or the male's alarm call. Desensitization of females to one of these signals (for example, the male eagle alarm call), also caused desensitization to the eagle vocalization itself. This finding provides evidence to support the idea that the female monkeys, upon hearing the male eagle alarm call, form a mental representation of an eagle, that they can then transfer and apply to the eagle vocalization (Zuberbuhler et al., 1999). This ability to form mental representations was later confirmed to be true in the case of visual stimuli as well (Arnold, Pohlner, & Zuberbühler, 2008). Referential calling with regard to the existence of a food source has been more enigmatic; it has only been shown conclusively (i.e., by the actual initiation of feeding behavior) in two species – the marmoset (*Callithrix geofffroyi*) and the chicken (C. S. Evans & Evans, 1999; Kitzmann & Caine, 2009). Conceptually, the idea of referential abilities in animal species is perhaps even more beneficial than it might seem at first glance. Landauer and Dumais (1997) postulate that it is possible to learn a considerable amount of language using induction - without explicit feedback. It seems that it would be extremely beneficial for the survival of any one individual monkey to recognize, for example, that a tiger is dangerous from only having experienced first hand the danger of a lion.

The ability to combine calls has also been observed in several species. Putty nosed monkeys (*Ceropithecus nictitans*) have two call types; however, they are able to arrange these calls into syntactically different combinations that, in turn, represent semantically different meanings (Arnold $\&$ Zuberbuhler, 2006b). A similar system has been found in two species of black and white colobus monkeys (*Colobus spp.*; Schel, Tranquilli, & Zuberbühler, 2009). Extending the parallel to humans even further, Campbell's monkeys (*Cercopithecus campelli campbelli*), have a communication system that involves (a) acoustic sounds serving as roots to a vocalization (akin to the "stem" in human language), and (b) sounds that can be alternatively fixed onto these stems – as with a human language morpheme (Ouattara, Lemasson, $\&$ Zuberbuehler, 2009). A system such as this is reminiscent of the recursive system held by some to be unique to humans. Lastly, white faced capuchin monkeys may encode their identity into food calls, allowing for others to make judgments on the benefit of attempting to join in a particular meal (Gros-Louis, 2008); this process combines both referential and cognitive abilities.

Teaching Language to Animals

The idea that we can teach our language to animals stems from research that has indicated that particular species possess higher cognitive abilities; thus, attempts to teach them should not be futile. Whether by cause or by effect, this means that much experimental research in this area is done with species such as primates to that humans "relate," and the most well-known experiments in animal communication are by far ones that attempted to communicate with animals via teaching them artificial language. Several of these programs have been highly successful (although at times controversial) – for example, Kanzi the bonobo (Savage-Rumbaugh & Lewin, 1994), Alex the African gray parrot (Pepperberg, 1999), and the dolphins of Kewalo Basin (Herman et al., 1984), all who have mastered the basics of human languages either in the form of actual words or symbols/gestures.

Evidence for the kind of cognitive complexity that would allow animals to learn human languages can be found in the theory of mind research (Forrester, 2008; Stuss, Gallup, & Alexander, 2001). Theory of mind, thought by some not to exist in non-human animals, is "thinking about thinking," or the awareness that a conspecific can know something about the knowledge of another conspecific. Tests of this ability have shown that primates have knowledge of both the amount of information a conspecific has, and the purpose of another's behavior (Hare, Call, Agnetta, & Tomasello, 2000; Hare, Call, & Tomasello, 2001). For example, subordinate chimpanzees will only move to obtain food when competing with an uninformed or misinformed dominant, or when the informed dominant has been replaced by a naïve animal (Hare, et al., 2000). Additionally, several species of non-human animals – bonobos, chimpanzees, elephants, dolphins, orangutans, and possibly gorillas – have passed the "mirror self recognition" (MSR) test (InoueNakamura, 1997; McCowan & Reiss, 2001; Patterson & Cohn, 1994; Plotnik, de Waal, & Reiss, 2006; Povinelli, et al., 1997; Stuss, et al., 2001; Westergaard & Hyatt, 1994). MSR involves understanding that a mirror reflection is specifically a reflection of the individual, and is thus used as an indicator of selfawareness (Gallup, 1970). The animals credited with this ability have all been (in most cases, quite obviously) observed engaging in self-directed behaviors while looking in a mirror.

Quantifying communication using information theory

A variety of techniques rooted in information theory (the quantification of information; Shannon, 1948) and other mathematical concepts (such as entropies, neural networks, and statistical regularities) have been shown to provide much insight into animal communication. In fact, experimental procedures as early as the 1970s attempted to understand how animals communicated via information theory (e.g., Menzel, 1973). These procedures assigned tasks or provided information to one member of a population; in order to complete the task or obtain a reward, it was necessary for the knowledgeable individual to pass this information on to others in the population. This technique has even been used to measure information transfer in ants. One elegant experiment showed the transfer of bits of information (turns in a maze along a path to get food, where one turn was equal to one bit of information), from scout ants to worker ants, to be reliable in the actual finding of the food by the workers (Reznikova, 2007).

Additionally, computer modeling has come to the forefront of research, with recent efforts to quantitatively detect, segment, and classify vocalizations in species including bottlenose dolphins (Buck $\&$ Tyack, 1993; Janik, 1999; McCowan, 1995), killer whales (*Orcinus orca*; Brown, Hodgins-Davis, & Miller, 2006; Deecke, Ford, & Spong, 1999), humpback whales (*Megaptera novaeangliae*; Suzuki, Buck, & Tyack, 2006), bats (*Microchiroptera spp*.; Skowronski & Harris, 2006), prairie dogs (*Cynomys gunnisoni;* Placer, Slobodchikoff, Burns, Placer, & Middleton, 2006), beaked whales (*Mesoplodon spp.*; Mellinger, 2008), and songbirds (Siegal & Varley, 2006).

The Role of Animal Models in Examining the Evolution of Language

Despite the fallacy that humans "evolved from" animals, there is merit in an evolutionarily comparative approach to the study of language – particularly one with a neuroscience perspective (Kuczaj & Kirkpatrick, 1993). The comparative approach gives, among other things, insight into the evolutionary pressures that have shaped our own cognitive processes.

It is well known that the human brain is lateralized for certain tasks. Some hypothesize that this lateralization evolved because the ability to process two "tasks" at once was extremely advantageous. For example, normal chicks are able to use their one eye in a foraging task, while simultaneously using their other eye to monitor their surroundings for predators (Hunsaker, Rogers, & Kesner, 2007). Chicks whose lateralization is disrupted during development by incubation in the dark are unable to carry out these tasks simultaneously (Hunsaker et al., 2007).

Studies have also shown that the asymmetry for language possessed by humans may also be present in other primates. Positron Emission Tomography (PET) has shown activity in the areas of the brain associated with conceptual representation and recognition of conspecifics in humans to also be present in the brains of awake rhesus macaques when they hear vocalizations from other macaques (Gil-Da-Costa, et al., 2004). This hemispheric asymmetry is also present in another species, the vervet monkey (*Cercopithecus aethiops*); however, the advantage is in the opposite hemisphere (left ear/right hemisphere, as opposed to right ear/left hemisphere). This finding supports the idea that asymmetry may have been advantageous for survival, adaptation, and evolution; however, the "details," for example, the particular side which houses the asymmetry, may be less important (Gil-Da-Costa & Hauser, 2006).

The mirror system hypothesis (Rizzolatti & Arbib, 1998) states that spoken language evolved from gesture (Arbib, 2005). Much of this theory is based on the primate homolog to Broca's area in humans, the F5 region. In this region are found mirror neurons, that are activated both when executing a movement and seeing another execute the same movement (Rizzolatti, Fadiga, Gallese, & Fogassi, 1996). As these are motor neurons, in a scenario such as this, the most likely precursor to the language area in the human brain would have been responsible for motor control. More recently, a similar class of neurons has been identified in birds that is activated both during singing and during audition, particularly when note sequences are within (or similar to) a songbird's repertoire (Prather, Peters, Nowicki, & Mooney, 2008).

Regardless of the developmental path, vocalizations of both humans and animals may respond to environmental pressures in a similar manner. The alarm calling behavior in Campbell's monkeys, discussed above, is established to be acoustically variant and semantically combinable across situations; in addition, it appears to respond to the direct needs of a particular population. When free living monkeys are compared to ones in captivity, the same rapidly rising, pulsed, call elements are used by both populations to create different alarm calls. Whereas free living individuals used these call elements to produce multiple, predator-specific alarm calls, captive individuals did not. The captive monkeys studied possessed one call, composed of these same acoustic elements - an alarm call for humans (Ouattara, Zuberbühler, N'Goran, Gombert, & Lemasson, 2009). While this discovery is, of course, additional evidence for referential signaling in this species, it also shows developmental plasticity of acoustic communication signals, a characteristic much studied in humans. It appears that despite different branches from our common ancestor, the ability to adapt acoustics to what is needed in a particular situation or lifestyle has been conserved in monkeys.

Finally, the FOXP2 gene was first identified in a family with a severe speech disorder and is often referred to as the "language gene," due to its suspected crucial role in the normal development of language (Lai, Fisher, Hurst, Vargha-Khadem, & Monaco, 2001). FOXP2 is present both in animals that vocalize and those that do not, and is also involved in motor coordination (including the muscles in the face responsible for vocal communication). Recent work on similarities between human and chimpanzee FOXP2 shows a difference in expression and regulation of several target genes (Konopka, et al., 2009). This work shows separate but parallel path for the development of FOXP2 and its targets; and in combination with information about language differences between humans and chimpanzees, will help in the exploration of congenital language deficits.

10

Implications for the Study of Human Language, Cognition, and Evolution

A similarity or consistency of language between humans and non-human animals would have many implications for evolutionary theory. The ability to compare languages across species would (a) allow the examination of cognitive and mechanical traits in language that are conserved across homologous species (such as humans and non-human primates) (Fitch, 2005; Zuberbuhler, 2005), and (b) permit testing of ideas that our linguistic abilities are modifications of a shared homologous trait, as opposed to novel occurrences (Lloyd, 2004). Perhaps more interesting, because of the lack of a common ancestor, is that linguistic similarities between humans and non-primates would indicate analogous situations in that language evolved in multiple phylogenetic lines (Fitch, 2005). From this we could hypothesize situations for which the trait of language ability would be selected. For example, a finding that marine mammals use semantics and a syntactic structure in their communications would provide evidence that at some point in the evolution of both humans and marine mammals, the environment supported the development of complex communication. It might then be possible to compare the evolutionary history of both species to determine what these conditions were and the mechanisms by which language developed. This comparison would speak to the importance of communication as a survival tactic, just as the analogous evolution of flight in birds, insects, and bats (mammals) speaks to the advantage of the development of flight. This is one of the strongest arguments for communication research involving species such as marine mammals, which is currently less abundant than that which deals with primates.

Language (or language-like) abilities in non-human animal species would, perhaps retrospectively*,* provide evidence for advanced cognitive mechanisms in these species. Researchers have provided evidence for hemispheric lateralization in animals with respect to several different cognitive abilities – a situation analogous to that of the human brain (for more information, see Kilian, Fersen, & Gunturkun, 2005; Ridgway, 2002; von Fersen, Schall, & Gunturkun, 2000; Yaman, Fersen, Denhardt, & Gunturkun, 2003), that in turn may be evidence indicative of complex cognition and development because of the increased substrate available for functional use. Investigations into the lateralization of communication in marine mammals would also be intriguing in light of Ridgway's (2002) evidence for the existence of

11

unihemispheric sleep in dolphins, for which the implications for communication have not yet been examined. For example, if aspects of dolphin brain function are strictly lateralized, does one hemisphere compensate for the processes that would normally be occurring in the "sleeping" hemisphere? If so, how is this done and can this compensation be induced in impaired humans? These possibilities further indicate the necessity for evolution of advanced anatomical and physiological features to support complexity in animal brains; it is very likely that this cognitive complexity could provide the framework for language (perhaps as an evolutionary spandrel, as per Gould and Lewontin, 1979), or, at the very least, an increased propensity for language development. As pointed out by Lloyd (2004), "none of the capacities that Kanzi [the bonobo used in many of Savage-Rumbaugh's experiments] used to perform these linguistic abilities was designed by natural selection for such tasks; rather, that was just a feature of Kanzi's brain, which could, under this extremely special environment [the research lab], learn to do those things" (pg. 583). Lloyd further alludes to themes common with the current "evo-devo" trend in ecology. Like pluripotent cells, cognitive brain tissue may have the theoretical capacity to develop to any level of ability; constrained only by the environment or rules surrounding it (Laundauer and Dumais, 1997, also speak of the constraints of rules on language development, that they appear to view as dangerously close to quashing the wide open semantic spaces of the mind). This evo-devo-esque spin on the development of language also may open the door a little wider for the idea that language has its roots in cognitive tasks like tool making or manual tasks like gesture (Lloyd, 2004).

The role of high dimensional models

High-dimensional memory models such as Hyperspace Analog to Language (HAL) and Latent Semantic Analysis (LSA) offer a neurally plausible architecture that can scale up to large computations as found in the brain (Landauer, Foltz, & Laham, 1998; Lund & Burgess, 1996). For example, semantic priming, which deals with the advantage a word has for retrieval if it is preceded by a related word (e.g., *cat* primes *dog*) may be largely due to how often words co-occur (Plaut, 1995); furthermore, semantic distances such as those measured by these models are very accurate indicators of retrieval time (Burgess, 1998; Lund & Burgess, 1996). It follows from this logic that global co-occurrence information better

represents human learning and the semantic continuum than local co-occurrence or simple frequency measures. Indeed, others have argued that HAL is a very promising new alternative to traditional models of semantics (Henry & Lucas, 2008; Hutchison, 2003). As the HAL model introduces a certain flexibility to language analysis, it seems appropriate that the approach should be applied to an area where flexible techniques and innovative thinking are vital.

Goals of this study

This set of three experiments was aimed at comparing syntax and structure in the vocalizations of three very different species – a bird, a sea mammal, and a land mammal. The perspective used is a very global one; instead of examining specific conditional probabilities, the HAL model examines language from a contextual perspective, which has not been attempted before and which may be necessary to hundreds of constraints involved in any sort of higher order language (Landauer and Dumais, 1997). This perspective may be able to provide new insights because the species compared have very different communication systems on the level of individual vocalizations; however, a broader analysis may reveal contextual similarities in communication. It is my hypothesis that each of these species will show signs of structure in their communication systems, and, further, that these structures can be characterized by contextual co-occurrences.

METHODS

Systems for Animal Communication Research

The research discussed here involves three types of animals – an African gray parrot (*Psittacus Erithacus*), humpback whales (*Megaptera novaeangliae*), and white mice (*Mus musculus*).

Research conducted with Cosmo, the African gray parrot, was done with several goals: (a) to determine whether Cosmo learned individual words or entire phrases, (b) to discover if there were changes in Cosmo's speech patterns/behavior when her owner, Betty Jean, was not present, and (c) to find out if Cosmo used a global syntax in her language. The first and third investigations are intimately linked. If

Cosmo learned individual words one at a time, then she would have to put them together to form the phrases in her repertoire – some of which were four to five words long. This would mean that Cosmo has a very workable pattern of global co-occurrence in her speech. A simple phrase such as "Cosmo wanna talk," could be permuted to "Cosmo wanna whistle," "Betty Jean wanna talk," "Cosmo wanna shower" and so forth. The Cosmo/Betty Jean and talk/whistle/shower sets are part of the global groups "names of people who live in the house" and "things Cosmo and Betty Jean do," respectively. Conversely, if Cosmo learned her repertoire as phrases, her repertoire would be less flexible on the word level, although one might find global co-occurrence in phrases such as "where are you," "I'm here," "there you are," and "come here" (contact calls). Lastly, a combination of the two might be possible, in which Cosmo used standard phrases and consistently altered only one word, for example, "that's birdie," "that's squirrel," and "that's doggie".

Many of the reasons for using marine mammals as a system to study animal communication and cognition have been detailed above. Bottlenose dolphins are naturally the most often used species for marine mammal research due to the relative ease of keeping them in captivity. Herman and colleagues, working with bottlenose dolphins, have examined the word order and syntactic abilities characteristic of simple human language, and have shown that dolphins understand that changes in these represent changes in meaning (Herman et al., 1984; Richards, Wolz, & Herman, 1984). The subjects in these studies were trained in either acoustic or gestural language, and showed comprehension of sentences with a variety of novel structural and syntactic features; these include word order changes, sentence reversals, and combinations of sentences (Herman, et al., 1984; Richards, et al., 1984). Field studies have shown vocal dialects in several species of large whales - sperm whales (*Physeter macrocephalus*), killer whales, and humpback whales in particular-- and longitudinal studies have further shown changes in these dialects over time and social groupings (Darling & Sousa-Lima, 2005; Deecke, Ford, & Spong, 2000; Eriksen, Miller, Tougaard, & Helweg, 2005; Rendell & Whitehead, 2003; Rendell & Whitehead, 2005). The research here seeks to add to the existing body of literature by integrating approaches that have been productive with human language investigations. Focusing on humpback whales takes advantage of the fact that vocalizations (songs) have already been shown to have a hierarchical nature (Payne & McVay, 1971), in

addition to the potential for geographic dialects. Goals for this portion of the study include a comparison of song units (and their co-occurrences) across three geographical locations and a search for patterns that might indicate syntax or structure.

Lastly, the examination of ultra-sonic songs of male mice is an opportunity to take advantage of a relatively new direction of research. Only recently has it been found that male mice "sing" ultrasonic courtship songs (Holy $\&$ Guo, 2005). Additionally, these songs appear to change with genetically abnormal mice. Studies are already investigating the usefulness of these discoveries for behavioral phenotyping of mouse models (Scattoni, Crawley, & Ricceri, 2009). The mouse model used, *Fmr1* (The Dutch-Belgian Fragile X Consortium, 1994), is used as a model for Fragile X Syndrome. Because there are language deficits in Fragile X Syndrome, the language deficits in the mice are of extreme interest. For example, discovering an inability in the genetically altered mice to correctly produce calls may not indicate an intellectual deficit; however, discovering an inability to create phrases through the combination of lexical items might.

HAL Methodology

The Hyperspace Analog to Language (HAL) model is a high-dimensional model that provides a method for the contextual analysis of language (Burgess, 1998; Lund & Burgess, 1996). HAL uses word order in language to compute co-occurrence values between words in a particular body of text (a *corpus*). The input to the model is a series of segmented words.

Before discussing the co-occurrence methodology, it is important to consider the overall plausibility of the input for such a model. The HAL model works because it is provided with a segmented stream of words, much like what infants hear during language development. Previous experiments have demonstrated that infants heavily rely on statistical co-occurrence information at the phonetic level in learning word segmentation (Aslin, Saffran, & Newport, 1999; Estes, Evans, Alibali, & Saffran, 2007; Saffran, et al., 2008). Furthermore, it has been demonstrated that the segmentation information in the speech stream can be modeled; a simple recurrent network (SRN) can utilize this phonetic information to

discover word boundaries (Cairns, Shillcock, Chater, & Levy, 1997; Christenson, Allen, & Seidenberg, 1998). Experiments comparing results from a SRN and HAL show that both models, when provided with the same input, produce virtually identical results (Burgess & Lund, 2000). Thus, it would appear vital that the input to HAL be in the form of segmented communication as well. The species discussed herein all have vocal repertoires in which semantic units are distinct from each other.

However, before being encoded by the HAL model, some of the vocalizations discussed here must be translated from acoustic data, segmented (in their electronic format), and, most importantly, classified. The most accurate method for doing this has been the topic of much research and debate (Clemins, Johnson, Leong, & Savage, 2005; Janik, 1999; Melendez, Jones, & Feng, 2006; Murray, Mercado, & Roitblat, 1998; Rickwood & Taylor, 2008; van der Schaar, Delory, Catala, & Andre, 2007), although the current favored techniques are segmentation by humans or by some variation on a self-learning neural network such as a Self Organizing Map (SOM).

In addition, none of the models currently in the literature are based on a global co-occurrence theory. HAL is a different kind of memory and language model, which, by using a global co-occurrence algorithm, is able to identify the similarities of a particular word's contextual uses across a large body of text (such as a language). For example, the words *cat* and *dog* often appear in the same sentence in human language (*I have a cat and a dog*). This is a local co-occurrence. However, *cat* and *dog* can also show a global co-occurrence pattern (*I have a cat that I'm in charge of feeding. She has a dog that she's in charge of feeding*). In global co-occurrence, *cat* and *dog* occur in the same context – in both sentences they are "the things that can be had and must be fed". This also makes them essentially (grammatically) substitutable. A traditional, local co-occurrence model would still identify *cat* and *dog* as being related , but would do so based only on the sentence *I have a cat and a dog.* In a more distinct example, the words *street* and *road* rarely occur in the same sentence, but are used in virtually the same contexts (*Make a left on that street. Make a left on that road*). The contextual similarity of the words *street* and *road* is reflective of their global co-occurrence, that would not be identified by a simple local co-occurrence procedure. While much valuable information can be obtained from both local co-occurrence models and

16

conditional probabilities, they do not capture higher-order contextual relationships because they do not encode words in this broader, contextual, sense (Burgess, 1998; Lund & Burgess, 1996).

Global co-occurrence values in the HAL model are computed by use of a sliding window (typically ten words long for human language corpuses), that assigns a co-occurrence value to each pair of words in the window based on the number of intervening words. A matrix is created by encoding these values (see Figure 1a for an example matrix). Co-occurrences between a particular word and those that precede it are encoded in rows, while those that follow it are encoded in the columns of the matrix.

Figure 1. a) Example HAL matrix of the sentence "Studying animal vocalizations is fun." Window size is five, co-occurrences between a particular word and those that precede it are encoded in rows, while those that follow it are encoded in the columns. b) Example co-occurrence vector for the word "animal" in the above matrix. Row co-occurrence values are followed by column values.

a. Example sentence: Studying animal vocalizations is fun.

b. Vector for "animal" -4000000432

By including co-occurrence values for words that occur both before and after a target word, the

model provides a contextual perspective beyond conditional probabilities or measures of entropy that only encode co-occurrences in one direction. Once a matrix is formed, each word can be represented by a vector comprised of its row co-occurrence values and its column cooccurrence values (see Figure 1b). Theses vectors can be visualized and grouped by using either multi-dimensional scaling or hierarchical cluster analysis. The placement of words in these visualizations is a function of the similarity of their contextually driven vectors

analysis was deemed most useful in visualization of clusters. Ward's analysis is unique from other methods of cluster analysis in that the clusters it creates are based on attempts to minimize the error sum of

(see Figure 2), and words

Figure 3.

squares between the two groups (Aldenderfer & Blashfield, 1984; Ward, 1963). This approach is particularly useful in visualization of a HAL analysis because the reduction to two dimensions naturally causes information loss, and, although the loss is much less than one might expect (Burgess, 1998; Lund $\&$ Burgess, 1996), Ward's method provides an ANOVA-like reliability for the clusters in high-dimensional space. One of the major disadvantages with using Ward's method is that it tends to give solutions with many small, distinct clusters (Aldenderfer & Blashfield, 1984). The analyses performed here were not troubled by this, which may provide additional support for the robustness of the data.

HAL parameters

l

When creating a HAL matrix and the resultant vectors, there are several options or parameters that can be set. The three options relevant to the experiments here are "window size," "cut," and "limit."

Window size controls the number of words³ on either side of the target word that are used calculate the actual encoding of the word into the memory matrix . It is a measure of the length of the sliding window. The default window size (and size that has been found to be most appropriate for use with human language) is 10. Smaller corpuses and/or corpuses in which less sophisticated co-occurrence is expected warrant smaller window sizes (Burgess, 1998; Lund & Burgess, 1996).

The cut function removes all words in a corpus that occur with a frequency at or below a certain level (for example, a cut at 3 removes all words that occur only once, twice, or three times in the corpus). This allows for the removal of words for which there are not enough occurrences to create fully coherent representations. By varying where the cut is with the size of the corpus, it is possible to normalize the corpuses by forcing HAL to focus only on the, say, top 75% most frequent words, regardless if one corpus has 10,000 words and is cut at 30 and another has 1,000 words and is cut at 2 (these numbers are were chosen at random for the sake of the example and should not be construed as mathematically sound).

 3 W hen working with human language, characters such as punctuation and numbers are included in the window as well; however, this is less of an issue with the animal corpuses

Limits serve to equalize frequency from the top down – in many corpuses (human or otherwise) a small set of words are a lot more frequent than others. The limit parameter tells HAL to "look" only at the first X number of instances of each word when calculating its co-occurrence, thereby controlling for a frequency effect (Burgess, 1998; Lund & Burgess, 1996).

Knowing when it's "The" Answer

One of the most frustrating parts of the experiments described here is the lack of confirmation of results. Beyond playback studies, which are beyond the scope of this project, it is hard to know for certain if a conclusion is correct, almost correct, on the right track, or not even in the same ballpark. The decisions made throughout with regard to model parameters and corpus selections are based on extensive reading of the literature, discussions with individuals who work directly with animals and computational models, and an extensive process of testing of model parameters. The assumption was made that, like all systems, the communication systems of the species in question move toward stability and regularity; thus, the less entropic a solution was, the more plausible it might be as an actual solution. This assumption has been used in other information theory experiments (Ferrer i Cancho, Riordan, & Bollobas, 2005; Ferrer i Cancho & Sole, 2003; McCowan, Doyle, Jenkins, & Hanser, 2005; Suzuki, et al., 2006). However, it should also be noted that the present experiments were conducted with the full appreciation that important characteristics of the communication systems could easily be overlooked or even be completely imperceptible to humans.

REFERENCES:

Aldenderfer, M. S., & Blashfield, R. K. (1984). *Cluster Analysis*. London: Sage.

- Arbib, M. A. (2005). From monkey-like action recognition to human language: An evolutionary framework for neurolinguistics. *Behavioral and Brain Sciences, 28*(2), 105-+.
- Arnold, K., Pohlner, Y., & Zuberbühler, K. (2008). A forest monkey's alarm call series to predator models. *Behavioral Ecology and Sociobiology, 62*(4), 549-559.
- Arnold, K., & Zuberbuhler, K. (2006a). The alarm-calling system of adult male putty-nosed monkeys, Cercopithecus nictitans martini. *Animal Behaviour, 72*(3), 643-653.
- Arnold, K., & Zuberbuhler, K. (2006b). Semantic combinations in primate calls. *Nature, 441*(7091), 303- 303.
- Aslin, R. N., Saffran, J. R., & Newport, E. L. (Eds.). (1999). *Statistical learning in linguistic and nonlinguistic domains*. Mahwah, New Jersey: Lawrence Erlbaum.
- Brown, J. C., Hodgins-Davis, A., & Miller, P. J. O. (2006). Classification of vocalizations of killer whales using dynamic time warping. *The Journal of the Acoustical Society of America, 119*(3), EL34- EL40.
- Byrne, R. W., Corp, N., & Byrne, J. M. E. (2001). Estimating the complexity of animal behaviour: How mountain gorillas eat thistles. *Behaviour, 138*, 525-557.
- Buck, J. R., & Tyack, P. L. (1993). A quantitative measure of similarity for tursiops truncatus signature whistles. *The Journal of the Acoustical Society of America, 94*(5), 2497-2506.
- Burgess, C. (1998). From simple associations to the building blocks of language: Modeling meaning in memory with the HAL model. *Behavior Research Methods, Instruments, & Computers, 30*(2), 188-198.
- Burgess, C., & Lund, K. (2000). The Dynamics of Meaning in Memory. In E. Dietrich & A. B. Markman (Eds.), *Conceptual and Representational Change in Humans and Machines* (pp. 117-156). Mahwah, New Jersey: Lawrence Erlbaum Associates.
- Cairns, P., Shillcock, R., Chater, N., & Levy, J. (1997). Bootstrapping word boundaries: A bottom up corpus-based approach to speech segmentation. *Cognitive Psychology, 33*, 111-153.
- Christiansen, M. H., Allen, J., & Seidenberg, M. S. (1998). Learning to segment speech using multiple cues: A connectionist model. *Language and Cognitive Processes, 13*(2/3), 221-268.
- Christiansen, M. H., & Kirby, S. (2003). Language evolution: consensus and controversies. *Trends in Cognitive Sciences, 7*(7), 300-307.
- Christiansen, M. H., & MacDonald, M. C. (2009). A usage based approach to recursion in sentence processing. *Language Learning, 59*(Suppl. 1), 126-161.
- Clemins, P. J., Johnson, M. T., Leong, K. M., & Savage, A. (2005). Automatic classification and speaker identification of African elephant (Loxodonta africana) vocalizations. *The Journal of the Acoustical Society of America, 117*(2), 956-963.
- Darling, J. D., & Sousa-Lima, R. S. (2005). Songs indicate interaction between humpback whale (Megaptera novaeangliae) populations in the western and eastern South Atlantic Ocean. *Marine Mammal Science, 21*(3), 557-566.
- de Vries, M. H., Monaghan, P., Knecht, S., & Zwitserlood, P. (2008). Syntactic structure and artificial grammar learning: The learnability of embedded hierarchical structures. *Cognition, 107*(2), 763- 774.
- Deecke, V. B., Ford, J. K. B., & Spong, P. (1999). Quantifying complex patterns of bioacoustic variation: Use of a neural network to compare killer whale (Orcinus orca) dialects. *Journal of the Acoustical Society of America, 105*(4), 2499-2507.
- Deecke, V. B., Ford, J. K. B., & Spong, P. (2000). Dialect change in resident killer whales: implications for vocal learning and cultural transmission. *Animal Behaviour, 60*, 629-638.
- Elman, J. L. (1990). Finding structure in time. *Cognitive Science, 14*, 179-211.
- Eriksen, N., Miller, L., Tougaard, J., & Helweg, D. (2005). Cultural change in the songs of humpback whales (Megaptera novaeangliae) from Tonga. *Behaviour, 142*, 305-328.
- Estes, K. G., Evans, J. L., Alibali, M. W., & Saffran, J. R. (2007). Can infants map meaning to newly segmented words?: Statistical segmentation and word learning. *Psychological Science, 18*(3), 254- 260.
- Evans, C. S., & Evans, L. (1999). Chicken food calls are functionally referential. *Animal Behavior, 58*, 307-319.
- Evans, C. S., & Marler, P. (1991). On the use of video images as social stimuli in birds: Audience effects on alarm calling. *Animal Behaviour, 41*, 17-26.
- Fehér, O., Wang, H., Saar, S., Mitra, P. P., & Tchernichovski, O. (2009). De novo establishment of wildtype song culture in the zebra finch. *Nature, 459*(7246), 564-568.
- Ferrer i Cancho, R., Riordan, O., & Bollobas, B. (2005). The consequences of Zipf's law for syntax and symbolic reference. *Proceedings in the Royal Society of London- Series B: Biological Sciences, 272*, 561-565.
- Ferrer i Cancho, R., & Sole, R. V. (2003). Least effort and the origins of scaling in human language. *Proceedings of the National Academy of Sciences, 100*(3), 788-791.
- Fitch, W. T. (2005). The evolution of language: A comparative review. *Biology & Philosophy, 20*, 193- 230.
- Fitch, W. T., & Hauser, M. D. (2004). Computational constraints on syntactic processing in a nonhuman primate. *Science, 303*(5656), 377-380.
- Forrester, G. S. (2008). A multidimensional approach to investigations of behaviour: revealing structure in animal communication signals. *Animal Behaviour, 76*(5), 1749-1760.
- Friederici, A. D., Bahlmann, J., Heim, S., Schubotz, R. I., & Anwander, A. (2006). The brain differentiates human and non-human grammars: Functional localization and structural connectivity. *Proceedings of the National Academy of Sciences, 103*, 2458-2463.
- Gallup, G. G. (1970). Chimpanzees: Self-recognition. *Science, 167*, 86087.
- Gentner, T. Q., Fenn, K. M., Margoliash, D., & Nusbaum, H. C. (2006). Recursive syntactic pattern learning by songbirds. *Nature, 440*(7088), 1204-1207.
- Gil-Da-Costa, R., Braun, A., Lopes, M., Hauser, M. D., Carson, R. E., Herscovitch, P., et al. (2004). Toward an evolutionary perspective on conceptual representation: Species-specific calls activate visual and affective processing systems in the macaque. *Proceedings of the National Academy of Sciences of the United States of America, 101*(50), 17516-17521.
- Gil-Da-Costa, R., & Hauser, M. D. (2006). Vervet monkeys and humans show brain asymmetries for processing conspecific vocalizations, but with opposite patterns of laterality. *Proceedings of the Royal Society B: Biological Sciences, 273*(1599), 2313.
- Griffin, A. S., Savani, R. S., Hausmanis, K., & Lefebvre, L. (2005). Mixed-species aggregations in birds: zenaida doves, Zenaida aurita , respond to the alarm calls of carib grackles, Quiscalus lugubris. *Animal Behavior, 70*(3), 507-515.
- Gros-Louis, J. (2008). Acoustic Analysis and Contextual Description of Food-Associated Calls in White-Faced Capuchin Monkeys (Cebus capucinus). *International Journal of Primatology, 27*(1), 273- 294.
- [Gould,](http://en.wikipedia.org/wiki/Stephen_Jay_Gould) S.J. & [R.C. Lewontin.](http://en.wikipedia.org/wiki/Richard_C._Lewontin) [\(1979\)](http://faculty.washington.edu/lynnhank/GouldLewontin.pdf). The Spandrels of San Marco and the Panglossian Paradigm: A Critique of the Adaptationist Programme. *Proceedings of the. Royal Society of London Series B, 205*, 581-598.
- Hare, B., Call, J., Agnetta, B., & Tomasello, M. (2000). Chimpanzees know what conspecifics do and do not see. *Animal Behaviour, 59*, 771-785.
- Hare, B., Call, J., & Tomasello, M. (2001). Do chimpanzees know what conspecifics know? *Animal Behaviour, 61*, 139–151.
- Hauser, M. D., Chomsky, N., & Fitch, W. T. (2002). The faculty of language: What is it, who has it, and how did it evolve? *Science, 298*(5598), 1569-1579.
- Hauser, M. D., & Glynn, D. (2009). Can free-ranging rhesus monkeys (Macaca mulatta) extract artificially created rules comprised of natural vocalizations? *Journal of Comparative Psychology, 123*(2), 161-167.
- Hauser, M. D., Newport, E. L., & Aslin, R. N. (2001). Segmentation of the speech stream in a non-human primate: statistical learning in cotton-top tamarins. *Cognition, 78*(3), B53-B64.
- Hauser, M. D., Weiss, D., & Marcus, G. (2002). Rule learning by cotton-top tamarins. *Cognition, 86*(1), B15-B22.
- Henry, K. S., & Lucas, J. R. (2008). Coevolution of auditory sensitivity and temporal resolution with acoustic signal space in three songbirds. *Animal Behaviour, 76*(5), 1659-1671.
- Herbranson, W. T., & Shimp, C. P. (2008). Artificial grammar learning in pigeons. *Learning & Behavior, 36*(2), 116-137.
- Herman, L. M., Richards, D. G., & Wolz, J. P. (1984). Comprehension of sentences by bottlenosed dolphins. *Cognition, 16*(2), 129-219.
- Hochmann, J. R., Azadpour, M., & Mehler, J. (2008). Do humans really learn A(n) B-n artificial grammars from exemplars? *Cognitive Science, 32*(6), 1021-1036.
- Hollen, L. I., & Manser, M. B. (2006). Ontogeny of alarm call responses in meerkats, Suricata suricatta: the roles of age, sex and nearby conspecifics. *Animal Behaviour, 72*(6), 1345-1353.
- Hollén, L. I., & Radford, A. N. (2009). The development of alarm call behaviour in mammals and birds. *Animal Behaviour, 78*(4), 791-800.
- Holy, T. E., & Guo, Z. (2005). Ultrasonic songs of male mice. *Plos Biology, 3*(12), 1-10.
- Howell, S. R., Jankowicz, D., & Becker, S. (2005). A model of grounded language acquisition: Sensorimotor features improve lexical and grammatical learning. *Journal of Memory and Language, 53*(2), 258-276.
- Hunsaker, M. R., Rogers, J. L., & Kesner, R. P. (2007). Behavioral characterization of a transection of dorsal CA3 subcortical efferents: comparison with scopolamine and physostigmine infusions into dorsal CA3. *Neurobiology of Learning and Memory, 88*(1), 127-136.
- Hutchison, K. A. (2003). Is semantic priming due to association strength or feature overlap? A microanalytic review. *Psychonomic Bulletin & Review, 10*(4), 785-813.
- Inoue-Nakamura, N. (1997). Mirror Self-recognition in nonhuman primates: A phylogenetic approach. *Japanese Psychological Research 39*(3), 266-275.
- Janik, V. M. (1999). Pitfalls in the categorization of behaviour: A comparison of dolphin whistle classification methods. *Animal Behavior, 57*, 133-143.
- Kilian, A., Fersen, L. v., & Gunturkun, O. (2005). Left hemispheric advantage for numerical abilities in the bottlenose dolphin. *Behavioral Processes, 68*, 179-184.
- Kitzmann, C. D., & Caine, N. G. (2009). Marmoset (Callithrix geoffroyi) Food-Associated Calls are Functionally Referential. *Ethology, 115*(5), 439-448.
- Kochanski. (2005). Is a phrase structure grammar the important difference between humans and monkeys? Retrieved December 12, 2007, from http://kochanski.org/gpk/papers/2004/FitchHauser/
- Konopka, G., Bomar, J. M., Winden, K., Coppola, G., Jonsson, Z. O., Gao, F., et al. (2009). Humanspecific transcriptional regulation of CNS development genes by FOXP2. *Nature, 462*(7270), 213- 217.
- Kuczaj, S. A., & Kirkpatrick, V. M. (1993). Similarities and differences in human and animal language research: Toward a comparative psychology of language. In H. L. Roitblat, L. M. Herman & P. E. Nachtigall (Eds.), *Language and Communication: Comparative Perspectives* (pp. 45-63). Hillsdale, New Jersey: Lawrence Erlbaum Associates.
- Lai, C. S. L., Fisher, S. E., Hurst, J. A., Vargha-Khadem, F., & Monaco, A. P. (2001). A forkhead-domain gene is mutated in a severe speech and language disorder. *Nature, 413*(6855), 519-523.
- Landauer, T. K., Foltz, P. W., & Laham, D. (1998). Introduction to Latent Semantic Analysis. *Discourse Processes, 25*, 259-284.
- Lloyd, E. (2004). Kanzi, evolution, and language. *Biology & Philosophy, 19*(4), 577-588.
- Lund, K., & Burgess, C. (1996). Producing high-dimensional semantic spaces from lexical co-occurrence. *Behavior Research Methods, Instruments, & Computers, 28*(2), 203-208.
- Manser, M. B. (2001). The acoustic structure of suricates' alarm calls varies with predator type and the level of response urgency. *Proceedings of the Royal Society B: Biological Sciences, 268*, 2315- 2324.
- McCowan, B. (1995). A new quantitative technique for categorizing whistles using simulated signals and whistles from captive bottlenose dolphins (Delphinidae, Tursiops truncatus). *Ethology, 100*, 177- 193.
- McCowan, B., Doyle, L. R., Jenkins, J. M., & Hanser, S. F. (2005). The appropriate use of Zipf's law in animal communication studies. *Animal Behavior, 69*(1), F1-F7.
- McCowan, B., & Reiss, D. (2001). The fallacy of `signature whistles' in bottlenose dolphins: a comparative perspective of `signature information' in animal vocalizations. *Animal Behavior, 62*(6), 1151- 1162.
- Melendez, K. V., Jones, D. L., & Feng, A. S. (2006). Classification of communication signals of the little brown bat. *The Journal of the Acoustical Society of America, 120*(2), 1095--1102.
- Mellinger, D. K. (2008). A neural network for classifying clicks of Blainville's beaked whales (Mesoplodon densirostris). *Canadian Acoustics, 36*(1), 55-59.
- Menzel, E. W. (1973). Chimpanzee spatial memory organization. *Science, 182*(4115), 943-945.
- Murray, S. O., Mercado, E., & Roitblat, H. L. (1998). The neural network classification of false killer whale (Pseudorca crassidens) vocalizations. *Journal of the Acoustical Society of America, 104*(6), 3626-3633.
- Newport, E. L., Hauser, M. D., Spaepen, G., & Aslin, R. N. (2004). Learning at a distance II. Statistical learning of non-adjacent dependencies in a non-human primate. *Cognitive Psychology, 49*(2), 85- 117.
- Ouattara, K., Lemasson, A., & Zuberbuehler, K. (2009). Campbell's Monkeys Use Affixation to Alter Call Meaning. *PLoS ONE, 4*(11), e7808.
- Ouattara, K., Zuberbühler, K., N'Goran, E. K., Gombert, J.-E., & Lemasson, A. (2009). The alarm call system of female Campbell's monkeys. *Animal Behaviour, 78*(1), 35-44.
- Owings, D. H., & Morton, E. S. (1998). *Animal vocal communication: A new approach*. Cambridge: Cambridge University Press.
- Patterson, F. G. P., & Cohn, R. H. (1994). Self-recognition and Self-awareness in Lowland Gorillas. In S. T. Parker, R. W. Mitchell & M. L. Boccia (Eds.). New York: Cambridge University Press.
- Payne, R., & McVay, S. (1971). Songs of humpback whales. *Science, 173*, 583-597.
- Pepperberg, I. M. (1992). Proficient performance of a conjunctive, recursive task by an African Grey parrot (Psittacus erithacus). *Journal of Comparative Psychology, 106*, 295-305.
- Pepperberg, I. M. (1999). *The Alex studies: Cognitive and communicative abilities of grey parrots.* Cambridge, MA: Harvard University Press.
- Perruchet, P., & Rey, A. (2005). Does the mastery of center-embedded linguistic structures distinguish humans from nonhuman primates? *Psychonomic Bulletin and Review, 12*(2), 313.
- Placer, J., Slobodchikoff, C. N., Burns, J., Placer, J., & Middleton, R. (2006). Using self-organizing maps to recognize acoustic units associated with information content in animal vocalizations. *The Journal of the Acoustical Society of America, 119*(5), 3140-3146.
- Plaut, D. C. (1995). Semantic and associative priming in a distributed attractor network. *Cognitive Science Proceedings*, 37-42.
- Plotnik, J. M., de Waal, F. B., & Reiss, D. (2006). Self-recognition in an Asian elephant. *Proceedings of the National Academy of Sciences, 103*(45), 17053–17057.
- Povinelli, D. J., Gallup, G. G., Eddy, T. J., Bierschwale, D. T., Engstrom, M. C., Perilloux, H. K., et al. (1997). Chimpanzees recognize themselves in mirrors. *Animal Behaviour 53*(5), 1083-1088.
- Prather, J. F., Peters, S., Nowicki, S., & Mooney, R. (2008). Precise auditory-vocal mirroring in neurons for learned vocal communication. *Nature, 451*(7176), 305-310.
- Randall, J. A., McCowan, B., Collins, K. C., Hooper, S. L., & Rogovin, K. (2005). Alarm signals of the great gerbil: Acoustic variation by predator context, sex, age, individual, and family group. *Journal of the Acoustical Society of America, 118*(4), 2706-2714.
- Randler, C. (2006). Red Squirrels (Sciurus vulgaris) Respond to Alarm Calls of Eurasian Jays (Garrulus glandarius). *Ethology, 112*(4), 411-416.
- Rendall, D., Owren, M. J., & Ryan, M. J. (2009). What do animal signals mean? *Animal Behaviour, 78*(2), 233-240.
- Rendell, L. E., & Whitehead, H. (2003). Vocal clans in sperm whales (Physeter macrocephalus). *Proceedings of the Royal Society of London Series B Biological Sciences, 270*(1512), 225-231.
- Rendell, L. E., & Whitehead, H. (2005). Spatial and temporal variation in sperm whale coda vocalizations: stable usage and local dialects. *Animal Behavior, 70*(1), 191-198.
- Reznikova, Z. (2007). Dialog with black box: using Information Theory to study animal language behaviour. *Acta Ethologica, 10*(1), 1-12.
- Richards, D. G., Wolz, J. P., & Herman, L. M. (1984). Vocal mimicry of computer-generated sounds and vocal labeling of objects by a bottlenosed dolphin, tursiops truncatus. *Journal of Comparative Psychology, 98*(1), 10-28.
- Rickwood, P., & Taylor, A. (2008). Methods for automatically analyzing humpback song units. *The Journal of the Acoustical Society of America, 123*(3), 1763-1772.
- Ridgway, S. H. (2002). Asymmetry and symmetry in brain waves from dolphin left and right hemispheres: Some observations after anesthesia, during quiescent hanging behavior, and during visual obstruction. *Brain, Behavior, and Evolution, 60*(5), 265-274.
- Rizzolatti, G., & Arbib, M. (1998). Language within our grasp. *Trends in Neurosciences, 21*(5), 188-194.
- Rizzolatti, G., Fadiga, L., Gallese, V., & Fogassi, L. (1996). Premotor cortex and the recognition of motor actions. *Cognitive Brain Research, 3*, 131-141.
- Saffran, J., Hauser, M. D., Seibel, R., Kapfhamer, J., Tsao, F., & Cushman, F. (2008). Grammatical pattern learning by human infants and cotton-top tamarin monkeys. *Cognition, 107*(2), 479-500.
- Savage-Rumbaugh, E. S. (1993). Language learnability in man, ape, and dolphin. In H. L. Roitblat, L. M. Herman & P. E. Nachtigall (Eds.), *Language and Communication: Comparative Perspectives*. Hillsdale, New Jersey: Lawrence Erlbaum.
- Savage-Rumbaugh, E. S., & Lewin, R. (1994). *Kanzi: The ape at the brink of the human mind*. New York: Wiley and Sons.
- Scattoni, M. L., Crawley, J., & Ricceri, L. (2009). Ultrasonic vocalizations: A tool for behavioural phenotyping of mouse models of neurodevelopmental disorders. *Neuroscience & Biobehavioral Reviews, 33*(4), 508-515.
- Schel, A. M., Tranquilli, S., & Zuberbühler, K. (2009). The alarm call system of two species of black-andwhite colobus monkeys (Colobus polykomos and Colobus guereza). *Journal of Comparative Psychology, 123*(2), 136-150.
- Scott-Phillips, T. C. (2010). Animal communication: insights from linguistic pragmatics. *Animal Behaviour, 79*(1), e1-e4.
- Seyfarth, R. M., Cheney, D. L., & Marler, P. (1980). Vervet monkey alarm calls: Semantic communication in a free-ranging primate. *Animal Behavior, 28*, 1070-1094.
- Shannon, C. (1948). A mathematical theory of communication, I and II. *Bell System Technical Journal, 27*, 379-423, 623-656.
- Siegal, M., & Varley, R. (2006). Aphasia, language, and theory of mind. *Social Neuroscience, 1*(3), 167 174.
- Skowronski, M. D., & Harris, J. G. (2006). Acoustic detection and classification of microchiroptera using machine learning: Lessons learned from automatic speech recognition. *The Journal of the Acoustical Society of America, 119*(3), 1817--1833.
- Slobodchikoff, C. N., Kiriazis, J., Fischer, C., & Creef, E. (1991). Semantic information distinguishing individual predators in the alarm calls of Gunison's prairie dogs. *Animal Behavior, 42*, 713-719.
- Soltis, J. (2009). What do animal signals do? *Animal Behaviour, 78*(6), 1485-1486.
- Stuss, D. T., Gallup, G. G., Jr., & Alexander, M. P. (2001). The frontal lobes are necessary for theory of mind. *Brain, 124*, 279.
- Suzuki, R., Buck, J. R., & Tyack, P. L. (2006). Information entropy of humpback whale songs. *The Journal of the Acoustical Society of America, 119*(3), 1849--1866.
- The Dutch-Belgian Fragile X Consortium. (Bakker CE, V. C., Willemsen R, van der Helm R, Oerlemans F, Vermey M, Bygrave A, Hoogeveen AT, Oostra BA, Reyniers E, et al.). (1994). *Fmr1* knockout mice: a model to study fragile X mental retardation. *Cell, 78*, 23-33.
- Toro, J. M., & Trobalon, J. B. (2005). Statistical computations over a speech stream in a rodent. *Perception & Psychophysics, 67*(5), 867-875.
- van der Schaar, M., Delory, E., Catala, A., & Andre, M. (2007). Neural network-based sperm whale click classification. *Journal of the Marine Biological Association of the UK, 87*(01), 35-38.
- von Fersen, L., Schall, U., & Gunturkun, O. (2000). Visual lateralization of pattern discrimination in the bottlenose dolphin (Tursiops truncatus). *Behavioral Brain Research, 107*, 177-181.
- von Frisch, K. (1967). *The dance language and orientation of bees*. Cambridge, MA: Harvard University Press.
- Ward, J. H. (1963). Hierarchical grouping to optimize an objective function. *Journal of the American Statistical Association, 58*, 236-244.
- Westergaard, G. C., & Hyatt, C. W. (1994). The responses of bonobos (Pan paniscus) to their mirror images: Evidence of self recognition *Human Evolution, 9*(4), 273-279.
- Yaman, S., Fersen, L. V., Denhardt, G., & Gunturkun, O. (2003). Visual lateralization in the bottlenose dolphin (Tursiops truncatus): Evidence for a population asymmetry? *Behavioral Brain Research, 142*(1-2), 109-114.
- Zuberbühler, K., Marc, N., Klaus, Z., Nicola, S. C., & Vincent, M. J. (2009). Survivor Signals: The Biology and Psychology of Animal Alarm Calling *Advances in the Study of Behavior* (Vol. Volume 40, pp. 277-322): Academic Press.
- Zuberbuhler, K. (2003). Referential signaling in non-human primates: Cognitive precursors and limitations for the evolution of language *Advances in the Study of Behavior* (Vol. 33, pp. 265-307).
- Zuberbuhler, K. (2005). The phylogenetic roots of language Evidence from primate communication and cognition. *Current Directions in Psychological Science, 14*(3), 126-130.
- Zuberbuhler, K., Cheney, D. L., & Seyfarth, R. M. (1999). Conceptual semantics in a nonhuman primate. *Journal of Comparative Psychology, 113*(1), 33-42.

CHAPTER 2: COSMO

INTRODUCTION

Past research on the intelligence of psittacines has been limited almost entirely to that of Irene Pepperberg and her African gray parrot, Alex. Pepperberg's work has often been criticized for drawing conclusions based on only one subject. However, Lloyd (2004) makes an excellent point that if even one member of a species is capable of a particular task, it must be assumed that the species is capable of the said task (i.e. possesses the appropriate neural/physiological/cognitive structures), regardless if individual members have developed these capabilities into useful (or even demonstrable) skills. The type of study employed by Pepperberg is an experimental paradigm called a power study, in which a single subject is used to prove that something is possible in a particular species. A power study is specifically not for purposes of comparison of abilities, it merely determines the existence of said abilities. In addition, a negative result of a power study does not preclude the ability in other members of the species (and thus the theoretically ability in all members) (Triana & Pasnak, 1981). Say Triana and Pasnak,

> "A power study, because it depends on the behavior of one or a few individuals to provide evidence for the existence of a given conceptual ability, does not permit inter- or intraspecies comparisons. Yet, tabulating or statistically comparing the relative success and failures of multiindividual samples of animals would not identify the intellectual *capacity* of a species satisfactorily and, in fact, is often quite misleading. If one individual can consistently and reliably demonstrate a given level of concept attainment, the performance is proof that this level is within the capacity of the species. Many failures by other individuals cannot invalidate this conclusion; they may identify the typical *performance* of a species, but not the conceptual *ability* of the species" (1981, pp. 135-136)

Pepperberg trains her parrots using a model/rival method – two lab assistants model a training session – asking and answering questions and modeling both correct and incorrect responses and their outcomes (Todt, 1975). Subsequently, the model or rival changes positions with the parrot, allowing every participant to play every role (Pepperberg, 1999). This is an interesting parallel to how a parrot might learn speech in a home on a day to day basis; by observing conversations (and outcomes thereof) and, when vocabulary is sufficiently developed, actively participating in them. Pepperberg's experiments have shown

that live tutors are necessary for learning referential English labels – parrots do not learn from videotapes, even when their attention is directed by human tutors and/or rewards are provided (Pepperberg, 1994; Pepperberg, Gardiner, & Luttrell, 1999; Pepperberg & McLaughlin, 1996).

After initially learning labels, Alex was taught the word "want" so that he might differentiate between naming and requesting. He easily generalized this to novel objects with no decrease in accuracy of the labels he had previously learned (Pepperberg, 1988). In fact, generalization of learned concepts has also been shown in blue-fronted parrots (*Amazona aestiva*), who demonstrated this ability in a task similar to one completed by cotton top tamarins (*Saguinus Oedipus*; de Mendonca-Furtado & Ottoni, 2008; Ghazanfar & Hauser, 1999). It has also been shown that parrots have a basic understanding of classes, and can understand when an object is a member of two different classes (i.e. "blue" and "round" as part of the classes "color" and "shape"). This particular type of learning is difficult for children, and young children often have much harder time learning the second label for an object than the first (Liittschwager $\&$ Markman, 1994). Parrots must be specifically taught to use color and label as a pair (Pepperberg $\&$ Wilcox, 2000), but are consequently able to answer questions directed at one of the two object classes (Pepperberg, 1983); Landauer and Dumais (1997) note that this difficulty with double labeling may be unique to humans – a result of overly specific constraints on language that in turn may cause children to make overly conservative assumptions about language and labeling.

There are other parallels to human language that can be found in Pepperberg's research. Alex has been recorded using spontaneous word play, including recombination of sounds and monologues (Pepperberg, Brese, & Harris, 1991); this spontaneous word play has been identified in human infants as key to private speech, one of two identified parts of monologue speech (Fusion, 1979). In human children, the meaning of words can be learned in two ways – fast mapping and full mapping. Fast mapping is the idea that children can learn the names of objects - and more importantly, understand that the names are used referentially for said objects – after just one exposure (Carey, 2001). In addition, this exposure to the object can be indirect – for example, an elimination task in which the child knows the names of all objects but one, and therefore can conclude that the novel name belongs to the novel object (Carey, 2001).

This indirect exposure is called emergent mapping (Wilkinson, Dube, & Mcilvane, 1998) and has also been formally identified in marine mammals and dogs (Herman, Richards, & Wolz, 1984; Kaminski, Call, & Fischer, 2004; Kastak & Schusterman, 2002; Schusterman & Krieger, 1984). Dogs have also been shown to learn object names by fast mapping at levels equivalent to three year old children (Kaminski et al., 2004). Schusterman and collegues (1984) were the first to use emergent mapping as a teaching process in non-human animals. After the initial learning of a small set of gestural signs, new "vocabulary" was introduced by pairing known gestures with novel ones. Teaching such as this requires a solid "match to sample" baseline (Wilkinson, et al., 1998). For an animal to identify a novel object by excluding other objects it must first be able to name the familiar objects (matching a known name to the sample object that is presented).

> "New object names were introduced by pairing the novel, and as yet unnamed object with an old, and already named, object. Under these conditions, both sea lions learned to associate or match the unfamiliar gesture with the unfamiliar object quite rapidly. Indeed, depending on the familiar-unfamiliar pairing, the match between a novel gesture and a novel object was frequently immediate as reflected by errorless performance." (Schusterman & Krieger, 1984, p. 13)

Pepperberg (1990) has identified a similar concept in parrots, dubbed referential mapping. Empirical data have also shown Alex understands that labels are built of individual units, which can be recombined to form novel, referential labels (Pepperberg, 2001, 2007). The idea of referential labeling has been demonstrated in other species of parrots as well; for example, it can be seen in the wild in speckled parrotlets (*Forpus conspicillatus*), a species that has referential calls for social companions or family members (Wanker, Sugama, & Prinage, 2005). This ability is closely linked with lexical substitution (Premack, 1976), which has been noted in marine mammals (Herman, et al., 1984; Schusterman & Krieger, 1986), nonhuman primates (Premack, 1976; Rumbaugh & Gill, 1977), and parrots (Pepperberg, 1990), and bears a striking resemblance to the substitutability of words in the HAL model. Further cognitive development leads to lexical creativity, or the combination of multiple words, each learned in independent contexts. When this is done intentionally and spontaneously in humans, it is called "segmentation" (Marler, 1970) or "combinatorial productivity" (Rexstad, et al., 1988).

There is also basic cognition research on psittacines and other birds. Several species of nonhuman animals – bonobos, chimpanzees, elephants, dolphins, orangutans, and possibly gorillas – have passed the "mirror self recognition" (MSR) test (Gallup, 1970; Inoue-Nakamura, 1997; McCowan & Reiss, 2001; Patterson & Cohn, 1994; Plotnik, de Waal, & Reiss, 2006; Povinelli, et al., 1997; Westergaard & Hyatt, 1994). As mentioned previously, MSR involves the understanding that a mirror reflection is specifically a reflection of the individual, and is thus used as an indicator of self-awareness (Gallup, 1970). These animals have all been observed engaging in self-directed behaviors when looking in a mirror. While parrots have not passed the MSR test, it has been shown that they can use a mirror to locate food that is hidden and cannot be found without the use (and understanding) of a mirror image (Pepperberg, 1995). Additionally, Stage 6 competence, or the ability to understand object permanence (Piaget, 1954), has been shown in psittacines and Eurasian jays (*Garrulus glandarius*) and, based on other studies, most likely exists in magpies (*Pica pica*) as well (Gomez, 2005; Pepperberg & Fink, 1990; Zucca, Milos, & Vallortigara, 2007). This ability is acquired by human infants between the ages of 18 and 24 months (Piaget, 1954).

Recent experiments have also investigated parrot's understanding of human concepts of music. When played music, one African grey was able to transpose notes accurately to an appropriate octave so that they could be sung back to the experimenter; the authors of the study hypothesize that this ability may be due to the variety of noises in a jungle setting and the demand for flexibility in order to be heard in different conditions (Bottoni, Masin, Lenti, Massa, & Massa, 2006; Bottoni, Massa, & Boero, 2003). These same experiments also showed that the parrot was able to insert musically appropriate sequences (i.e., ones in the right key) of its own into the song. In addition to singing, there have been experiments with dancing birds. Patel (2006) theorizes that, due to links between the auditory and motor systems, only animals whose brains are capable of complex vocal learning – such as humans and parrots – are able to learn beat synchronization. Later experimental research based on this hypothesis supports the idea – a sulphur-crested cockatoo (*Cacatua galerita eleanora*) was able to synchronize dancing movements to the beat of music, and was able to alter her beat with changes in the tempo of the song (Patel, Iverson, Bregman, Schultz, & Schultz, 2008). Studies such as these which reveal the abilities of parrots to

understand and process music will be integral to studying language from a comparative and evolutionary perspective (Fitch, 2006).

Contact calls, used by birds in the wild to keep in touch with their mates (Cruickshank, Gautier, & Chappius, 1993), are reflected in domesticated parrots and their owners (Colbert-White, 2009). Interestingly, there is a degree of convergence between pairs with respect to contact calls, both before and after pairing. There is evidence that initial pairing is due to preliminary similarity in calls (Moravec, Striedter, & Burley, 2006) – a difficult parallel to make for pair bonds between domestic parrots and humans – however there is also evidence for a great deal of convergence of contact calls after pairing (Moravec et al., 2006; Scarl & Bradbury, 2009). In cases such as this an already designated pair of parrots – or, in the case of this study, a parrot and its owner – will develop a set of common calls that are used to locate each other when out of visual contact (Bergman & Reinisch, 2006). Additionally, there is evidence that pairs possess multiple, acoustically distinct calls (Cortopassi & Bradbury, 2006). As discussed in the results of this paper, the subjects of study do, in fact, possess a number of different contact calls, and they not only occur most often in situations of visual separation, but have high levels of global co-occurrence as well.

Several other species of non-human animals have displayed abilities that may be similar to those domesticated parrots display. For example, Kanzi, a juvenile bonobo, learned language spontaneously as a result of being in the room during his mother's training (Savage-Rumbaugh & Lewin, 1994), just as parrots likely learned much of their language by overhearing conversation (see above discussion of Pepperberg's model-rival method for teaching language). Studies on domestic dogs (*Canis familiaris*) may also prove to be applicable, as they are similar to parrots in that they are domesticated pets. There is evidence that domestic dogs not only match their owner's voice to face, but that they also develop a representation of the owner's face upon hearing his/her voice. In an experimental situation, dogs looked longer at photos of strangers shown to them after hearing their owner's voice than they did photos of the owner, suggesting they were expecting the photo to match the representation they had conjured after hearing the voice (Adachi, Kuwahata, & Fujita, 2007). In a study comparing the ability of wolves and dogs to read human

cues to the location of hidden food, puppies raised by (domestic) mothers were more successful at reading cues than wolves raised by humans. The authors of the study speculate that this could be a result of genetic selection in domestic dogs for communication with humans (Hare, Brown, Williamson, & Tomasello, 2002). In addition, a subsequent study showed that dogs living in shelters (i.e. ones which were not pets) are able to understand a very basic pointing task, in which the experimenter held the point position, but not a task in which the experimenter retracted the point, a task that dogs living as pets are able to understand. However, it was subsequently shown that these shelter dogs were able to learn, with additional trials, the more complicated pointing task (Udell, Dorey, & Wynne, 2010). This again supports the hypothesis that interaction with humans may expose cognitive capacity that animals posses, but that they have had no use for in previous circumstances (Lloyd, 2004). It does not seem farfetched to hypothesize that similar skills have developed in parrots, which, like dogs, are domesticated animals which naturally live and feed in groups; and therefore naturally would need to both recognize and read the signals of others in their group.

The emergent perspective on language acquisition posits that language is learned not from an innate set of rules, but from the context and environment that surrounds us daily (Elman, 1991, 1995; O'Grady, 2008; Schoenemann, 1999). A parrot's ability to learn language provides substantial support for this hypothesis; and if the parrot is in fact learning language (as opposed to mere imitation), then the most logical explanation is that it is doing so via an emergent process. It would be very hard to claim that we, as humans, share an innate grammatical, genetic, language mechanism with parrots. Emergent theory proposes that, instead, language is learned in relation (or by co-occurrence with) the environment; and a parrot's exposure to language is fairly similar to that of a child's. Parrot owners often narrate what they are doing for their birds, have short conversations with them, speak on the telephone in their presence, and even use "mother-ese" when addressing them (Kanzi the bonobo also appears to have learned to parse and comprehend human language in this indirect way (Lloyd, 2004)). Language is shaped by the environment, and, a la evolution, similar environments require similar adaptations.

One of the first goals of this study was to determine if a distinction could be made between Cosmo's use of words and phrases; does Cosmo learn individual words that are substitutable within similar phrases (global co-occurrence), or does Cosmo learn static phrases that must learned for every situation she

encounters? For example, has Cosmo learned to say "Cosmo wanna ________," or must she learn "Cosmo wanna peanut," "Cosmo wanna grape," and "Cosmo wanna talk" each as a separate item? The global cooccurrence model being used, HAL, is specifically suited to this question; if the former hypothesis is true, HAL will create a high dimensional cluster of "things Cosmo wants," such as peanut, grape, and talk. In addition, a secondary goal of this study was to examine if Cosmo uses words that are appropriate to the situation she is in, and to provide support for the conclusions of Colbert-White (2009), who found this to be the case.

METHODS

Subject

This study was based on the vocalizations of a 6 year old African gray parrot by the name of Cosmo. Cosmo is owned by Dr. Betty Jean Craige (henceforth BJ), Professor of Comparative Literature and Director of the Willson Center for Humanities and Arts at the University of Georgia (Craige, 2010). All data were collected between October 2007 and August 2008 in the home of BJ in Athens, Georgia. Data were collected in one hour sessions, and four sessions were combined to create a data set for a particular condition. Extra sessions were recorded so that anomalous sessions (for example, ones in which BJ received a phone call or left the room) could be discarded. For details on the specific equipment and logistics of data collection, see Colbert-White (2009). Transcription of the speech of Cosmo and BJ was conducted by Erin Colbert-White (ECW) of the University of Georgia. The author coded eight minutes of each condition (Alone, In, and Out) to check reliability, which was determined to be $\kappa = .65, .85,$ and .69, respectively for each condition. As there is currently no standard for measuring inter-rater reliability in animal behavior (Kaufman & Rosenthal, 2009), human standards were used, and by human clinical standards, these indicate good to excellent agreement (Cicchetti & Sparrow, 1981). Data were then errorchecked by ECW and files were created containing complete dialogue for each session, only Cosmo's speech in each session, and only BJ's speech in each session. Cosmo's entire repertoire can be found in appendix A, and the frequency counts used in these experiments can be found in appendix D.

Conditions

There were three conditions examined. In, in which BJ was in the same room as Cosmo (and conversed freely and normally); Out (in which BJ was home, but in a different room than Cosmo, and again conversed freely and normally, albeit at a greater distance); and Alone (in which BJ was not at home and Cosmo was by herself, with the exception of two dogs). In the Out condition, BJ did not speak enough in order to build a HAL matrix. Therefore, analyses were done for the following corpuses –

> In, both speakers In, only Cosmo's speech In, only BJ's speech Out, both speakers Out, only Cosmo's speech Alone, only Cosmo's speech

Cosmo's vocalizations also included a significant number of sounds – bird calls, dog barks, telephone sounds, etc. As a result, corpuses were run with and without Cosmo's sounds (in order to determine if the event sounds were being used to convey meaning). "Phrase" and "word" corpuses were also run. This was an effort to determine whether Cosmo was learning speech as single words, or as phrases ("I love you" vs. "I," "love," and "you")

A variety of permutations of HAL settings were tested (for a discussion of reasons for trying a variety of HAL settings, see the general introduction to this paper). Based on these results, plus particular characteristics of each corpus (for example, length or frequency of individual items), the following parameters for each type of corpus were used –

> phrases and sounds – cut 3, limit 10, window size 10 phrases and no sounds – cut 2, limit 10 window size 10 words and sounds – cut 10, limit 30, window size 10 words and no sounds – cut 5, limit 30, window size 10

For a discussion of the "cut," "limit," and "window size" parameters, refer to the general introduction to this paper. The limit parameters are higher on the "words" corpuses because they were significantly longer than the "phrases" corpuses. Window size 10 was chosen as a starting point for all corpuses specifically because it is the default HAL setting and has been shown to be appropriate for human language (Burgess, 1998; Lund & Burgess, 1996), and Cosmo's vocalizations are based on human speech.

Visualization

HAL output (vectors) were visualized using Ward's Cluster Analysis (Ward, 1963). Ward's analysis differs from other cluster analysis methods because it is based on joining clusters with the goal of minimizing information loss. This is done by minimizing the error sum of squares. This analysis was chosen because of its similarity to an ANOVA, in addition to the advantage that it provided very distinct clusters with clear cut off points.

Ward's clusters also provide definitive cluster patterns, so determination of where to divide clusters is generally not an issue (Aldenderfer & Blashfield, 1984). For better visualization, clusters were transposed from the cluster analysis dendrogram to an excel spreadsheet. By manipulating the spreadsheet, data could be examined with reference to condition and corpus parameters, and be examined for global and local co-occurrences, and novel grammatical structures and utterances.

Decisions to identify the final corpus

At this point in the analysis it became clear that sounds (notated in capital letters, such as the sound "BARK" as opposed to the word "bark") were an integral part of Cosmo's vocabulary. Sounds did not separate from words, instead they were incorporated into clusters according to subject; for example, phone sounds and phone words were clustered together. As a result, the decision was made to exclude the "no sounds" corpuses.

The Cluster

Analyses obtained from this procedure at window size 10 were very tightly layered, which in turn resulted in less distinct clusters (see Figure 4). This seemed to indicate that if Cosmo were using global co-occurrence in her speech, the long distance dependencies between individual words were not as long as with humans. As this made sense, the data

were run again, changing the window size parameter to 3. These data showed more independent clusters that were far simpler to distinguish from each other.

It also became clear at this time that the "only Betty Jean" and "both" conditions were less useful than expected. The vocabulary used by both Cosmo and BJ was exactly the same, and as the HAL analysis involves a calculation across all instances in which the word is used, it was not possible for HAL's encoding mechanism to distinguish Cosmo's utterances from BJ's in the "both" condition. The corpus resulting from the "only Betty Jean" condition, originally intended for comparison purposes, was determined to be both unrepresentative of BJ's normal speech (and thus of less use for a comparison), and too small for useful HAL analysis.

After these determinations, the final corpus parameters used for analysis (in both word and phrase form) were Cosmo only, with sounds, cut 3, limit 10, window 3.

Substitution corpus

Later in the experiment, a third type of corpus was developed, called the "substitution corpus." In this corpus, all phrases that were variations on approximately the same sentiment were replaced by one, common, phrase. For example, "Cosmo's a good bird," "Cosmo's a good, good bird," and "Cosmo is a good bird" were all represented in the corpus as "Cosmo's a good bird." These corpuses were run on the parameters already established for the other corpuses.

RESULTS AND DISCUSSION

Corpus analyses

For the final HAL analysis, three forms of the corpus were used – words, phrases, and substitutions. For examples of cluster analysis results, see Figure 5.

General trends

In general, as the input to HAL lengthened, i.e. moved from word to phrase, clusters became more general. When input was on the word level, HAL clusters showed specific use of global co-occurrence and within-sentence context. At a phrase level, clusters appeared to be "topical" – dealing with, for example, phone related contexts. At the substitution level, which essentially collapsed the members of each of these topical clusters into one representative phrase, there was much less organization to be seen.

The Word Level Corpus

Sounds appear to play a very important role in Cosmo's vocalizations in the Alone condition. Her vocalizations in this condition feature a large cluster composed entirely of sounds, indicating the sounds are integrated throughout her vocabulary when she is alone (bear in mind, items occurring in the same cluster share context, they do not necessarily occur in the same sentences or phrases). Potentially, this could be similar to bilingualism in humans; these are the sounds that come naturally to Cosmo, however they have less communicative value when BJ is present and are therefore given a much less prominent place in Cosmo's speech when she is around. However, much like a human bilingual would take notes in his or her

native language instead of the one being used in the immediate environment; Cosmo may revert to her favored vocalization style when she is not interacting with BJ.

Figure 5. Sample clusters from a) Only Cosmo, In, words; b) Cosmo, Alone, words; c) Only Cosmo, Out, phrases; d) showing contextual co-occurrence within a cluster.

In all three conditions tested, global co-occurrence clusters reflecting different contextual usages of words were present. The most common of these clusters was of "things Cosmo wants." In the In condition, for example, this is represented by a cluster of the words "whi (presumably whistle), whistle, talk, come, cuddle, shower, go." All of these words are preceded by "wanna" in Cosmo's speech and are thus, in a very simplified sense, interchangeable over the category "things Cosmo wants." This is representative of a global co-occurrence pattern. There is also evidence of a "go" cluster in all three conditions.

The Phrase Level Corpus

Using Cosmo's speech in the HAL model in the form of phrases provided a new perspective. Cosmo has multiple spoken permutations of the same phrase, thus creating an abundance of synonyms, and, in turn a co-occurrence, due to the natural substitutability of synonyms. For example, just as "street" and "road" have the very similar meaning but would not be used in the same sentence, "we're gonna go for a walk" and "okay we're gonna go for a walk," or "DOG BARK SEQUENCE" and "DOG WHINE SEQUENCE" similarly seem to serve the same contextual purpose.

In the Alone Condition, Cosmo's speech was situationally appropriate. Of the 1185 phrases uttered by Cosmo in this condition (exclusive of phrases used 3 or fewer times), phrases from a "good Cosmo/bad Cosmo" class found elsewhere were completely lacking. Additionally, there were only two phrases from the "Cosmo wants" class, occurring a total of 16 times out of the 1185 total utterances. Lastly, vocalizations from the "contact calls" class were variations on "hello" and "goodbye"; they were not utterances such as "where are you" or duet whistles that request or elicit a response from BJ. All of these examples indicate an awareness that BJ is not present to respond to Cosmo's demands, reprimand or reinforce Cosmo, or to engage in conversation. Results from a previous study suggested the same situational awareness after comparing the In condition to a Company condition (in which BJ was in the room, but ignoring Cosmo and paying attention to another person in the room, a condition not analyzed in this study). In the Company condition, there was also a dramatic decrease in the amount of interactive language Cosmo used as compared to the In condition (Colbert-White, 2009).

The Out condition shows strong "contact call," "dog" and "phone" clusters. Contact calls are specific to BJ – they almost always elicit a response in which she whistles back to Cosmo or verbally identifies her location (I'm here) (Colbert-White, 2009). This may be Cosmo's attempts to contact her "flock," as duet calls such as these are known to be used for bonding in wild parrots (Cruickshank, et al., 1993). In addition Cosmo routinely interacts with the dogs, and therefore, dog contact calls such as barking (for lack of a better name for them), we can only suppose, are intended to attract the dog's attention. Three instances in this corpus provide examples of HAL identifying a situation unknown to the researcher and later confirmed by BJ. The first is the "wolf whistle," that consistently fell within the "contact call" cluster. It was confirmed with BJ, post hoc, that the wolf whistle is indeed used in a call and response manner by herself and Cosmo. Secondly was the presence of the strong "phone" cluster in the Out condition. While contact calls and calls to the dogs might serve to keep Cosmo in touch with others in the house, phone sounds did not seem to fit the pattern. However, upon further discussion with BJ, it appears that Cosmo will "make the phone ring" when BJ is out of the room (for example, when she gets in the shower or just as she leaves the house), as this causes BJ to come back into the room with Cosmo. Cosmo has been known to confess to the trick ("that's Cosmo"), showing a conscious awareness and intent to bring BJ into the room. Lastly, Cosmo's vocalizations showed she uses the phrase "hi Tom," although BJ knows no-one by the name of Tom. HAL analysis placed "hi Tom" within a contextual cluster that was easily recognizable to BJ as a very routine morning phone conversation that occurs with a person by the name of "Joan." The placement of the "hi Tom" vocalization within this cluster (and the absence of the name Joan), may indicate that "hi Tom" is a mispronunciation of "hi Joan."

The Substitutions corpus

Due to the abundance of variations on each phrase that occurs in the corpus, an additional corpus was run through HAL, in which all phrases that dealt with the same topic were grouped as the same. For example, the sounds PHONE RING and ANSWERING MACHINE, plus phrases such as "you have reached" were all re-named as "phone." This corpus showed much less organization than any of the others. It appears that the collapsing of similar phrases in the corpus created too much difference between

individual units, thus disallowing substitutability or co-occurrence. There were two notable occurrences, however, that inform us that the integrity of the methodology was maintained (see Figure 5d). As the substitutions were done by hand, it was inevitable that some phrases were missed. The continued existence of these synonymous phrases was able to provide validation by their own continued clustering; for example, the phrases "fine thanks how are you" and "fine thank you." In addition, groups of contact calls stayed together, for example DUET WHISTLE, WOLF WHISTE, and "come here." Because these calls were semantically diverse, they were not combined in the substitutions; however, they remained in the same contextual cluster because the model was consistent methodologically.

Novelties

During the course of the analysis several novel structures and unique combinations of words were spotted. As HAL is not a model intended to find novelties in semantics, this section discusses findings that were noted during the course of working with the HAL results.

Unique constructions

Examination of Cosmo's speech shows consistent use of constructions that must have been of Cosmo's own invention. Very often, Cosmo will use "that's wanna grape" instead of "wanna grape." Because Cosmo is able to use "that's" for identification purposes ("that's bark," "that's squirrel"), this novel construction may come from a generalization of "that's" to the "wanna grape" phrase; in a sense making "wanna grape" a noun. Cosmo also uses "here I are" as a contact call, again displaying a grammar of her own concoction; this is not a phrase BJ would have uttered. Cosmo also may have learned to use the word "don't" on her own – she says "Cosmo don't want to be a good bird," a construction for which there does not seem to be an opportunity to learn by mimicry, given its lack of grammaticality and reflexive nature. She has also inserted the words "don't" in other contexts, for example, the phrase "doggies don't bark."

These unique constructs provide further evidence for the hypothesis that global co-occurrence is present in Cosmo's speech patterns. The ability to parse words in and out of sentences correctly (or nearly so) shows an understanding that each word is an individual unit that has a specific meaning. More importantly, it shows an understanding that a single word can be appropriate in multiple sentences or contexts – a basic building block for semantic global co-occurrence. If it is the case, as the BJ claims, that Cosmo was not overtly taught the use of "don't" and that "don't" was not used in interaction with Cosmo, then it would appear that this word has been learnt by induction. Landauer and Dumais (1997) make a strong case for induction as the learning mechanism in early childhood vocabulary acquisition. They further argue that induction in this case can be embodied in a global co-occurrence model such has HAL (or in their case, LSA).

Humor

Although there is no way to specifically identify humor in Cosmo's vocalizations, she routinely makes utterances that sound in every way like humor. For example, Cosmo has learned the following phrases: "Cosmo has feathers," "Betty Jean has clothes," and "Mary has fur," (Mary is one of the dogs). "Playing" with these phrases has become a favorite "joke" of Cosmo's; she interchanges the direct objects (consistent with global co-occurrence as they are substitutable), and announces "Mary has feathers!" followed by "Noooooo! LAUGH, Mary has fur!" In addition, Cosmo will tease BJ in a variety of ways – the most interesting of which involves calling BJ over to her cage for a kiss and then ducking back into the cage (and out of range) at the last minute. Cosmo will do this multiple times and with appropriate pauses for BJ to resume her activities in between. The idea that Cosmo is using and understanding humor is especially intriguing in light of what it implies with regards to her cognitive abilities, and further investigating will be extremely interesting.

Word Meaning

The Cosmo corpus also provided several examples of Cosmo's ability to grasp word meaning. To begin, very existence of the clusters shows that meaning is clearly reflected in the statistical regularity of

her speech. In addition, this clustering shows Cosmo's ability to use words referentially in a reliable fashion – all the words in, for example, the "phone cluster" are a reference to the same object. This is not unlike a child's learning to understand that there can be two labels for the same object. This is not an easy skill for children, and it would have been difficult for Cosmo to have learned that "bark" and "woof," for example, label the exact same thing (Liittschwager & Markman, 1994). However, the co-occurrence results provided by HAL do provide cautious support for this.

In addition, there is some evidence that Cosmo engages in a certain amount of word play; an advanced skill which requires understanding of word meaning and the relationship between words and their contexts (Pepperberg et al., 1991). For example, it is possible that Cosmo understands that "good" and "bad" have opposing meanings. BJ relates anecdotal evidence in which she says "Cosmo's a bad bird," and Cosmo responds "Cosmo wanna be a good bird." Cosmo's "phone jokes" are an even more complex example. BJ's answering machine has always said "you have reached (XXX) XXX-XXXX." When Cosmo began to imitate the machine, she first only imitated up to the area code (i.e. You have reached XXX). Later the vocalization changed and Cosmo began using the telephone number without the area code. She would say "You have reached XXX-XXXX." Subsequently, Cosmo continued with variations on the message that were both novel and appropriate in context and meaning. She began to say "You have reached bird," "You have reached Betty Jean," "You have reached Cosmo" and "You have reached me." The substituting of words with different specific meanings (bird, Betty Jean, Cosmo, me) but that all belong to the same grammatical class ("person" nouns), again shows the effect of global co-occurrence on Cosmo's vocalizations.

.

REFERENCES:

Adachi, I., Kuwahata, H., & Fujita, K. (2007). Dogs recall their owner's face upon hearing the owner's voice. *Animal Cognition, 10*, 17-21.

Aldenderfer, M. S., & Blashfield, R. K. (1984). *Cluster Analysis*. London: Sage.

- Bergman, L., & Reinisch, U. S. (2006). Parrot vocalization. In A. U. Luescher (Ed.), *Manual of parrot behavior* (pp. 219-223). Ames: Blackwell Publishing.
- Bottoni, L., Masin, S., Lenti, D., Massa, B., & Massa, R. (2006). Teaching a musical code to a parrot: Frequency discrimination and the concept of rhythm in a Grey Parrot (Psittacus erithacus). *Advances in Bioacoustics 2, 47*(3), 75-86.
- Bottoni, L., Massa, R., & Boero, D. L. (2003). The grey parrot (Psittacus erithacus) as musician: an experiment with the Temperate Scale. *Ethology Ecology & Evolution, 15*(2), 133-141.
- Burgess, C. (1998). From simple associations to the building blocks of language: Modeling meaning in memory with the HAL model. *Behavior Research Methods, Instruments, & Computers, 30*(2), 188-198.
- Carey, S. (2001). Cognitive foundations of arithmetic: Evolution and ontogenisis. *Mind & Language, 16*(1), 37-55.
- Cicchetti, D. V., & Sparrow, S. S. (1981). Developing criteria for establishing interrater reliability of specific items: Applications to assessment of adaptive behavior. *American Journal of Mental Deficiency, 86*, 127-137.
- Colbert-White, E. N. (2009). *An African Grey parrot's vocal production varies across social context.* Masters of Science, University of Georgia, Athens, Georgia.
- Cortopassi, K. A., & Bradbury, J. W. (2006). Contact call diversity in wild orange-fronted parakeet pairs, Aratinga canicularis. *Animal Behaviour, 71*(5), 1141-1154.
- Craige, B.J. (2010)*. Conversations with Cosmo: At Home with an African Grey Parrot*. Santa Fe: Sherman Asher Publishing.
- Cruickshank, A. J., Gautier, J. P., & Chappius, C. (1993). Vocal mimicry in wild African Grey Parrots *Psittacus erithacus*. *Ibis, 135*, 293-299.
- de Mendonca-Furtado, O., & Ottoni, E. B. (2008). Learning generalization in problem solving by a bluefronted parrot (Amazona aestiva). *Animal Cognition, 11*(4), 719-725.
- Elman, J. L. (1991). Distributed representations, simple recurrent networks, and grammatical structure. *Journal of Machine Learning 7*(2-3), 195-225.
- Elman, J. L. (1995). Language as a dynamical system. In R. F. Port & T. van Gelder (Eds.), *Mind as Motion: Explorations in the Dynamics of Cognition*. Cambridge: MIT Press.
- Fitch, W. T. (2006). The biology and evolution of music: A comparative perspective. *Cognition, 100*(1), 173-215.
- Fusion, K. (1979). The development of self-regulating aspects of speech: A review. In G. Zivon (Ed.), *The development of self-regulation through private speech*. New York: Wiley.
- Gallup, G. G. (1970). Chimpanzees: Self-recognition. *Science, 167*, 86087.
- Ghazanfar, A. A., & Hauser, M. D. (1999). The neuroethology of primate vocal communication: substrates for the evolution of speech. *Trends in Cognitive Sciences, 3*(10), 377-384.
- Gomez, J. C. (2005). Species comparative studies and cognitive development. *Trends in Cognitive Sciences, 9*, 118-125.
- Hare, B., Brown, M., Williamson, C., & Tomasello, M. (2002). The domestication of social cognition in dogs. *Science, 298*, 1634-1636.
- Herman, L. M., Richards, D. G., & Wolz, J. P. (1984). Comprehension of sentences by bottlenosed dolphins. *Cognition, 16*(2), 129-219.
- Inoue-Nakamura, N. (1997). Mirror Self-recognition in nonhuman primates: A phylogenetic approach. *Japanese Psychological Research 39*(3), 266-275.
- Kaminski, J., Call, J., & Fischer, J. (2004). Word learning in a domestic dog: Evidence for "fast mapping". *Science, 304*(5677), 1682-1683.
- Kastak, C. R., & Schusterman, R. J. (2002). Sea lions and equivalence: Expanding classes by exclusion. *Journal of the Experimental Analysis of Behavior, 78*, 449-465.
- Kaufman, A. B., & Rosenthal, R. (2009). Can you believe my eyes? The importance of inter-observer reliability statistics in observations of animal behaviour. *Animal Behaviour, 78*, 1487-1491.
- Landauer, T. K., & Dumais, S. T. (1997). A solution to Plato's problem: The latent semantic analysis theory of acquisition, induction, and representation of knowledge. *Psychological Review, 104*(2), 211- 240.
- Liittschwager, J. C., & Markman, E. M. (1994). Sixteen- and 24-month-olds' use of mutual exclusivity as a default assumption in second-label learning. *Developmental Psychology, 30*(6), 955-968.
- Lloyd, E. (2004). Kanzi, evolution, and language. *Biology & Philosophy, 19*(4), 577-588.
- Lund, K., & Burgess, C. (1996). Producing high-dimensional semantic spaces from lexical co-occurrence. *Behavior Research Methods, Instruments, & Computers, 28*(2), 203-208.
- Marler, P. (1970). A comparative approach to vocal learning: Song development in white-crowned sparrows. *Journal of Comparative and Physiological Psychology, 71*, 1-25.
- McCowan, B., & Reiss, D. (2001). The fallacy of `signature whistles' in bottlenose dolphins: a comparative perspective of `signature information' in animal vocalizations. *Animal Behavior, 62*(6), 1151- 1162.
- Moravec, M. L., Striedter, G. F., & Burley, N. T. (2006). Assortative Pairing Based on Contact Call Similarity in Budgerigars, Melopsittacus undulatus. *Ethology, 112*(11), 1108-1116. doi: doi:10.1111/j.1439-0310.2006.01267.x
- O'Grady, W. (2008). The emergentist program. *Lingua, 118*(4), 447-464.
- Patel, A. D. (2006). Musical rhythm, linguistic rhythm, and human evolution. *Music Perception, 24*, 99- 104.
- Patel, A. D., Iverson, J. R., Bregman, M. R., Schultz, I., & Schultz, C. (2008). *Investigating the humanspecificity of synchronization to music.* Paper presented at the Conference on Music Perception and Cognition, Sapporo, Japan.
- Patterson, F. G. P., & Cohn, R. H. (1994). Self-recognition and Self-awareness in Lowland Gorillas. In S. T. Parker, R. W. Mitchell & M. L. Boccia (Eds.). New York: Cambridge University Press.
- Pepperberg, I. M. (1983). Cognition in the African Grey parrot: Preliminary evidence for auditory/vocal comprehension of the class concept. *Animal Learning and Behavior, 11*(2), 179-185.
- Pepperberg, I. M. (1988). An interactive modeling technique for acquisition of communication skills separation of labeling and requesting in a psittacine subject. *Applied Psycholinguistics, 9*(1), 59- 76.
- Pepperberg, I. M. (1990). Referential mapping: A technique for attaching functional significance to the innovative utterances of an African Grey parrot (Psittacus erithacus). *Applied Psycholinguistics, 11*, 23-44.
- Pepperberg, I. M. (1994). Vocal learning in grey parrots (Psittacus erithacus): Effect of social interaction, reference, and context. *Auk, 111*(2), 300-313.
- Pepperberg, I. M. (1995). Mirror use by African grey parrots (Psittacus erithacus). *Journal of Comparitive Psychology, 109*, 182-195.
- Pepperberg, I. M. (1999). *The Alex studies: Cognitive and communicative abilities of grey parrots.* Cambridge, MA: Harvard University Press.
- Pepperberg, I. M. (2001). Millennium Review: Avian Cognitive Abilities. *Bird Behavior, 14*, 51-70.
- Pepperberg, I. M. (2007). Grey parrots do not always 'parrot': the roles of imitation and phonological awareness in the creation of new labels from existing vocalizations. *Language Sciences, 29*(1), 1- 13.
- Pepperberg, I. M., Brese, K. J., & Harris, B. J. (1991). Solitary sound play during acquisition of english vocalizations by an African Gray Parrot (Psittacus-Erithacus) - Possible parallels with childrens monologue speech. *Applied Psycholinguistics, 12*(2), 151-178.
- Pepperberg, I. M., & Fink, M. S. (1990). Object permanence in four species of psittacine birds: An African Grey parrot (Psittacus erithacus), an huger mini macaw (Ara maracana), a parakeet (Melopsittacus

undulatus), and a cockatiel (Nymphicus hollandicus). *Animal Learning and Behavior, 18*(1), 97- 108.

- Pepperberg, I. M., Gardiner, L. I., & Luttrell, L. J. (1999). Limited contextual vocal learning in the grey parrot (Psittacus erithacus): the effect of interactive co-viewers on videotaped instruction. *Comparative Psychology, 113*(2), 158-172.
- Pepperberg, I. M., & McLaughlin, M. A. (1996). Effect of avian-human joint attention on allospecific vocal learning by grey parrots (Psittacus erithacus). *Journal of Comparitive Psychology, 110*, 286-297.
- Pepperberg, I. M., & Wilcox, S. E. (2000). Evidence for a form of mutual exclusivity during label acquisition by grey parrots (Psittacus erithacus)? *Journal of Comparative Psychology, 114*(3), 219-231.
- Piaget, J. (1954). *The construction of reality in the child*. New York: Basic Books.
- Plotnik, J. M., de Waal, F. B., & Reiss, D. (2006). Self-recognition in an Asian elephant. *Proceedings of the National Academy of Sciences, 103*(45), 17053–17057.
- Povinelli, D. J., Gallup, G. G., Eddy, T. J., Bierschwale, D. T., Engstrom, M. C., Perilloux, H. K., et al. (1997). Chimpanzees recognize themselves in mirrors. *Animal Behaviour 53*(5), 1083-1088.
- Premack, D. (1976). *Intelligence in ape and man*. Hillsdale, NJ: Erlbaum.
- Rexstad, E. A., Miller, D. D., Flather, C. H., Anderson, E. M., Hupp, J. W., & Anderson, D. R. (1988). Questionable multivariate statistical inference in wildlife habitat and community studies. *Journal of Wildlife Management, 52*, 794-798.
- Rumbaugh, D., & Gill, T. V. (1977). Lana's acquisition of language skills. In D. M. Rumbaugh (Ed.), *Language Learning by a Chimpanzee: The Lana project* (pp. 165-192). New York: Academic.
- Savage-Rumbaugh, E. S., & Lewin, R. (1994). *Kanzi: The ape at the brink of the human mind*. New York: Wiley and Sons.
- Scarl, J. C., & Bradbury, J. W. (2009). Rapid vocal convergence in an Australian cockatoo, the galah Eolophus roseicapillus. *Animal Behaviour, 77*(5), 1019-1026.
- Schoenemann, P. T. (1999). Syntax as an emergent characteristic of the evolution of semantic complexity. *Minds and Machines, 9*(3), 309-346.
- Schusterman, R. J., & Krieger, K. (1984). California Sea Lions are capable of semantic comprehension. *The Psychological Record, 34*, 3-23.
- Schusterman, R. J., & Krieger, K. (1986). Artificial language comprehension and size transposition by a California Sea Lion (Zalophus californianus). *Journal of Comparative Psychology, 100*, 348-355.
- Todt, D. (1975). Social learning of vocal patterns and modes of their applications in Grey parrots. *Zeitschrift fur Tierpsychologie, 39*, 178-188.
- Triana, E., & Pasnak, R. (1981). Object permanence in cats and dogs. *Animal Learning & Behavior, 9*, 135- 139.
- Udell, M. A. R., Dorey, N. R., & Wynne, C. D. L. (2010). The performance of stray dogs (Canis familiaris) living in a shelter on human-guided object-choice tasks. *Animal Behaviour, 79*(3), 717-725.
- Wanker, R., Sugama, Y., & Prinage, S. (2005). Vocal labelling of family members in spectacled parrotlets, Forpus conspicillatus. *Animal Behavior, 70*(1), 111-118.
- Ward, J. H. (1963). Hierarchical grouping to optimize an objective function. *Journal of the American Statistical Association, 58*, 236-244.
- Westergaard, G. C., & Hyatt, C. W. (1994). The responses of bonobos (Pan paniscus) to their mirror images: Evidence of self recognition *Human Evolution, 9*(4), 273-279.
- Wilkinson, K. M., Dube, W. V., & Mcilvane, W. J. (1998). Fast mapping and exclusion (emergent matching) in developmental language, behavior analysis, and animal cognition research. *The Psychological Record, 48*(3), 407-422.
- Zucca, P., Milos, N., & Vallortigara, G. (2007). Piagetian object permanence and its development in Eurasian jays (Garrulus glandarius). *Animal Cognition, 10*, 243-258.

CHAPTER 3: HUMPBACK WHALES

INTRODUCTION

Payne and McVay (1971) first demonstrated that the sounds made by humpback whales while "singing" were organized and sequential. After it was established that these patterns existed, characterization began. The first attempts to characterize song showed syllables that could be combined into motifs, motifs that could be combined into create phrases, and phrases that were joined into themes. Phrases and motifs were found to be extremely redundant, yielding a distinct hierarchical structure; for example, a particular phrase might be composed of one motif repeated three times, and three repeats of the phrase might be dubbed a theme (Winn & Winn, 1978). When these phrases and motifs were compared over the years, differences in the form of additions or subtractions of syllables or syllable types were noted. Small differences in song were also noted across locations; however, as the study site was small and therefore the absolute distance between locations was also small, no conclusions could be drawn (Winn & Winn, 1978). However, on a larger scale, very definitive geographic differences were later found between songs recorded in the North Atlantic, North Pacific, and South Pacific (Winn et al., 1981).

The general consensus was, and remains, that songs are used primarily for courtship purposes, as they are sung almost exclusively by males in breeding season. A recent study showed that 58% of male humpback whale singers were found associating with conspecifics, and singers were more likely both to join up with and stay longer with groups of whales containing mother-calf pairs and no other males (Smith, Goldizen, Dunlop, & Noad, 2008). However, other hypotheses do exist: (a) that the song is part of a search mechanism, possibly even long-range sonar (Frazer & Mercado, 2000); (b) that song plays a part in sexual selection, for example, the ability to sing a lengthy song without breathing could be a sign of greater fitness (Chu, 1988); (c) that song creates a social organizational structure, possibly even one that occurs cooperatively among males in mating season (Darling, Jones, & Nicklin, 2006); or (d) that song is indicative of a whale's position in a dominance hierarchy (Darling, 1983). See Parsons et al. (2008) for an excellent review of these and other hypotheses.

While humpbacks may be the most well-studied singers, there are other Mysticetes (baleen whales) - for example, bowhead whales (*Balaenoptera mysticetus*) and fin whales (*Balaenoptera physalus*) - that are suspected of singing for courtship purposes (Stafford, Moore, Laidre, & Heide-Jorgensen, 2008; Watkins, Tyack, & Moore, 1987).

Odontocetes (toothed whales) are also known to vocalize (although not in the form of song), and current data show more complex, socially dependent systems of vocalizations. However, Odontocetes tend to be much more social than Mysticetes, often traveling and/or hunting in groups and having a social order dictating movements within and between groups. For example, killer whales possess a set of vocalizations used by all members of the species, in addition to subsets that are specific to social or cultural groups (Eliades & Wang, 2008; Riesch, Ford, & Thomsen, 2006; Weiss, Symonds, Spong, & Ladich, 2007). The "cultural clan" hypothesis was first coined with reference to another species of toothed whale, the sperm whale, and details changes in vocalizations across social groups can be traced matrilineally (Rendell & Whitehead, 2001). And, of course, bottlenose dolphins – also toothed whales – are well known for their complex social systems and their signature whistles, suspected to be used for individual identification (Caldwell & Caldwell, 1965). Odontocetes tend to be more surface active than Mysticetes as well, making it feasible to conduct observational studies linking behavior to vocalization (Deecke, 2006; Frantzis & Alexiadou, 2008; Riesch et al., 2008). Baleen whales such as humpbacks tend to travel alone or in small groups, dive deep, stay underwater longer, and feed at deeper depths (Clapham, 2000); thus, data collection beyond the acoustics of song is nearly impossible. These factors may be the largest reasons why there is as yet no definitive answer on the purpose of humpback whale song.

One of the main focuses of the research presented here are the geographical differences in song. Differences in vocalizations have been identified across geographical or ecological areas in many species of marine mammals: Atlantic spotted dolphins (*Stenella frontalis*; Baron, Martinez, Garrison, & Keith, 2008), Atlantic bottlenose dolphins (Baron, et al., 2008), fin whales (*Balaenoptera physalus*; Delarue, Todd, Parijs, & Di Lorio, 2009), and blue whales (*Balaenoptera musculus*; Berchok, Bradley, & Gabrielson, 2006). Recently, vocal differences such as these were also found in a primate, the pygmy marmoset (*Callithrix pygmaea*; de la Torre & Snowden, 2009). If sufficient behavioral data cannot be

obtained to aid in the understanding or purpose of song, it is hoped that differences in song over geographical area (or even across time) will help us to understand how song is transmitted between whales, if dialects exist, and, most importantly, what key aspects of the song are, based on what properties are evolutionarily conserved. Towards this end, there is some evidence for the conservation of adaptive vocalizations from songbirds; in a species of songbird, the black capped chickadee (*Poecile atricapillus*), successful memes (pieces of song) persist as traditions across the population. These successful memes appear to be carried by older, larger birds (hypothesized as a function of body condition, but potentially also a function of longevity, and, therefore, of an individual's experience). Other memes studied were unsuccessful and quickly went extinct. These memes tended to be confined to small geographic areas and used less frequently (Baker & Gammon, 2008). For this reason, variation over geographical distance may be a key component of cultural development of vocalization. The work here is with song recorded in three geographic locations that happen to be aligned. Support for geographical dialects might, for example, be evidenced by a song pattern in the middle geographic area (Puerto Rico), that is a combination of styles from the two other areas.

In addition to the basic rhythmic structure, early observers noted other properties of humpback whale song; for example, average sequence lengths of 4-10 units, and transitional phrases located between themes that included elements of both of the themes they served to separate (Payne & McVay, 1971). Recently, others have used ideas from mathematics, physics, and engineering to further these initial observations; for example, Suzuki et al. (2006) used an entropy analysis to conclude that the most probable average length of a sequence within a song is 6-8 units. In addition, a new variable was recently examined – the duration between the units. While the duration of the units themselves seems to be consistent, the time between units seems to be highly dependent on the units to follow and/or other units in the pattern. This is hypothesized to be one of the ways humpbacks may be able to recall and repeat such large portions of song (Handel, Todd, & Zoidis, 2009). This is not particularly surprising, given the human phenomenon of

chunking, which allows us to remember large amounts of information by dividing and remembering it as manageable "chunks" of information; thus remembering multiple groups, rather than specific instances, of information (Miller, 1956). If this parallel were true, the whales could be remembering songs by learning groups or patterns of sequences or units, rather than individual units. This would make memorization and recall easier, in addition to extending the animal's capacity for information storage.

METHODS

The corpus

The corpus used in this experiment stemmed from vocalization data obtained from the Macauley Library (Cornell Laboratory of Ornithology) and was classified by a Self Organizing Map (SOM; Kohonen, 1982). Original data were obtained via DVD data disks and included 325 distinct recordings made by 17 scientists. The recording dates ranged from 1964 to 2006 and included locations in both Atlantic and Pacific Oceans. Twelve songs from three locations were originally selected for analysis (three recordists, years ranging from 1970-1976), although only 11 songs were used in the final analysis (reasons for this are discussed below). The internal sequence order of each song was maintained (with some exceptions, discussed below).

The SOM

Prior to analysis, the elements of the humpback whale song were classified by a 25-unit SOM. The SOM used 53 acoustic features to create vector representations of each unit of vocalization, and then used a competitive learning algorithm to classify the vocalization into one of 25 distinct nodes or units of vocalization. All work concerning the translation of acoustic units to a written sequence, in addition to the creation of the SOM, was done by Sean Green; for more information on the procedure used to create the SOM, see Green, Mercado, Pack, & Herman, 2007. A 100 node SOM was also attempted; however it appeared that the extra nodes provided no additional information. Artificial neural networks, of which the SOM is an example, are gaining in popularity for the classification of animal vocalizations and have

become fairly standard in the literature for a variety of species (Deecke, Ford, & Spong, 1999; Kirschel, et al., 2009; Mellinger, 2008; Placer, Slobodchikoff, Burns, Placer, & Middleton, 2006; Pond, Darre, Scheifele, & Browning, 2010; Rickwood & Taylor, 2008; Selin, Turunen, & Tanttu, 2006; van der Schaar, Delory, Catala, & Andre, 2007).

HAL parameters

As the corpus used in this study was large (a total of several thousand acoustic units), a default window size of 10 was deemed appropriate (Lund & Burgess, 1996). In this corpus, unit frequency ranged from as high as 500 to 600 occurrences of a particular unit to as few as 14 occurrences of a unit – although in most cases the minimum number of occurrences of any particular unit in a corpus was 150. In cases such as this, it is often beneficial to "limit" the matrix at the mean or median frequency. The limit acts as a quota; as HAL moves through the corpus calculating co-occurrence values, it disregards any occurrences of a particular unit after that unit's limit has been reached. The limit on all of the matrices used was $250⁴$, unless otherwise indicated.

Mixing the corpus

Because it was advantageous to limit the maximum unit occurrence in the HAL matrix at 250, it was necessary to "mix" the corpus to avoid problems with songs that contained particularly high numbers of any specific unit. For example, if the first song in the corpus contained 250 occurrences of a particular unit, HAL would reach the limit for that unit almost immediately, and, thus, would ignore any occurrences of that unit in any other song for the remainder of the corpus. In order to avoid this problem, and to balance the first and second halves of the songs, songs were "mixed" as follows (parts A and B designate the first and second halves of each song)

 $\frac{1}{4}$ This limit was chosen because prior experimentation indicated that the median of the unit frequencies was the most appropriate value to use when limiting a matrix.

Split 1 Song1, partA Song2, partB Song3, partA Song4, partB etc… Split2 Song1, partB Song2, partA Song3, partB

Song4, partA etc…

The two splits were then concatenated to create a final corpus to be used in the experimental procedure. A template was created and used each time a corpus needed to be mixed. Additionally, the splits created were used in the split-half reliability checks discussed later.

HAL analysis

The mixed corpus was subjected to HAL analysis as described previously. The result of this analysis was a 25-dimensional space containing 25 vector representations--one for each unit ("word"). Following the procedures discussed in the introduction, these vectors were visualized via Ward's Cluster Analysis and mapped onto the original corpus.

Confirmatory analyses and final corpus selection

When a HAL analysis is used with human language, there is no need for confirmatory analysis. Because we know the language, it makes sense to us that "cat" and "dog" should be more likely to co-occur (either globally or locally) than "cat" and "file." This luxury is not afforded when working with a corpus comprised of animal vocalizations, and, therefore, two separate techniques were used to validate the results.

Song removal

Three new corpuses were created by removing songs. Song numbers 117762 and 128296, henceforth referred to as song62 and song96, were removed, as they appeared to be more irregular due to inordinately high proportions of a particular unit or group of units (92% of song62 was composed of four units, 45% of song96 was composed of one specific unit) (see discussion in Miksis-Olds, Buck, Noad, Cato, & Stokes, 2008). Song96 was also much shorter than any other song. These removals created the corpuses "without117762" (or wo62), "without128296" (or wo96), and "without117762and128296" (wo62and96), in addition to the "full" corpus. A comparison of all four corpuses was used as a test for robustness of the procedure, in addition to being used in the final corpus selection process detailed below.

Song62 and song96 were removed in the acoustic stage, prior to unit classification by the SOM. Because of this procedure, however, there was an inherent problem with comparing the four corpuses. When classification is done by different SOMs, the identification of each acoustic unit (i.e. the unit's "name") is different. For example, a particular acoustic unit could have been called unit1 by the full SOM, unit16 by the wo62 SOM, unit22 by the wo96 SOM, and unit25 by the wo62and96 SOM.

To solve this problem, color coding was used as a way of marking clusters when they were output from the clustering procedure using the corresponding HAL vectors. Each of the clusters created by the cluster analysis was assigned a color. For example, in Figure 6, a cluster analysis of the full corpus, the cluster containing unit4, unit5, and unit9 is assigned the blue color. Consequently, all of the units 4, 5, and 9 in the full corpus are colored blue. In addition, because the temporal order within the corpuses was maintained, the acoustic units were still ordered the same, regardless of what they were called. In this way it was possible to approximate equivalent clusters in the four corpuses by reading horizontally (i.e. examining acoustic sounds that occurred at the same place in the sequence) and labeling their respective, equivalent, clusters by color, despite the different unit names (see Figure 7). This procedure could be used for comparison across corpuses by individual song as well as along the complete corpus, and was used throughout the analyses in this dissertation.

B's, as discussed before. However, the two splits were now treated as two separate corpuses, instead of being concatenated to one corpus. Because there is no accepted statistical method to compare categorical data, Cohen's kappa (1960) was used as an experimental approximation. Cohen's kappa is an inter-rater reliability statistic used to compare agreement between two raters who code behavioral observations. In this case, the two versions of cluster membership (the full and one of the split halves) were each considered to be a "rater" and the cluster membership for each unit was considered the rating for each particular behavior. As a result, the model was created such that two "raters" (the two versions of cluster membership) were being compared on 25 "instances of behavior" (the 25 units), for which they had assigned one of eight "types of behavior" (the clusters).

Figure 7. Mapping of the color coding scheme onto the corpus. In this example, the same song is color coded with clusters obtained from each of the 4 corpuses (i.e. the "full" corpus grouped unit 10 and unit 19, while the "wo62" corpus grouped unit1, unit6, unit12, and unit13). As the sequence is maintained in all cases, each cell in a particular row is the same acoustic unit, regardless of the unit label assigned by the SOM. HAL, grouping the units by global co-occurrence, should maintain the same order with regard to cluster membership, and this can be read across rows as matching color patterns. Note this is only a small portion of a song.

Types of Analysis

Two types of analysis were done, one that examined the frequency of occurrence of units and classes, and one that examined the overall entropy of the songs. Frequency of occurrence of each class was examined as a measure of change in song composition and perhaps dialect, whereas entropy analysis was performed to establish that only a certain number of the sequences that were possible actually existed (that in turn establishes that they are not random), and then to identify and compare these sequences across songs. The algorhythm for entropy analysis was developed and executed by Aaron Seitz of the University of California, Riverside.

Frequency Analysis

Although it is unknown if frequency of occurrence of unit or class plays a role in humpback whale communication, there is some precedent for it being studied as a variable. Suzuki et al. (2006) used frequency of occurrence to estimate the true distribution of units in humpback song, thus generalizing over a particular area. In killer whales, frequencies of occurrence of whistles within the sequence and transition patterns between whistles in sequences are nonrandom (Riesch et al., 2008). Frequency also plays a large part in calculations of conditional probabilities in other studies of humpback whale song (Green et al., 2007).

Entropy Analysis

Working on the assumption that the greater the organization, the closer to the correct clustering, an analysis was performed on each of the songs individually, using the clusters produced by building a HAL matrix using the entire corpus. This was done initially to identify empirically if any of the songs were in fact anomalous (song62 and song96 were suspected to be and because of this were removed for a test of robustness; however they could not be removed entirely without an empirical justification).

The analysis also provided a comparison of the sequence organization in the corpus to that of a random sequence. For example, when examining sequences that are four units in length in a completely random corpus, one would expect 256 (4*4*4*4) different sequences to occur, with the only constraint being the frequency of occurrence of each unit. A fewer number of distinct sequences would indicate a degree of organization. Entropy analysis provides that information, along with the actual identification of the sequences that are found.

Upon identifying the sequences that existed within each song (via the entropy analysis algorithm), further data analysis was based on sequences that occurred five or more times in a particular song (henceforth referred to as "the sequences found").

The Elman Corpus

Because one of the goals of this study was finding semantic patterns within humpback whale song, it seemed relevant to perform a similar procedure on human language. The corpus chosen was one created by Elman (1990) when developing his Simple Recurrent Network (SRN). This corpus was chosen because it has been subject to HAL analysis previously and, despite a completely different learning mechanism (although both learn by encoding contexts), HAL yielded similar results to the SRN (Burgess & Lund, 2000). In addition, the corpus consists of approximately the same number of words (29) as there were units in the humpback whale song (25). The Elman Corpus underwent HAL analysis just as the humpback

whale song was, although many of the elaborate confirmatory procedures did not have to be undertaken since the language and categories were known. HAL vectors were subjected to cluster analysis, and clusters were color coded and mapped on to the original corpus, just as had been done in the case of the whale song (see Figure 8).

RESULTS

Perhaps most crucially, HAL was able to produce distinct cluster patterns from the SOM output, showing that the units, as classified by the SOM, do indeed have some form of organization. Because the HAL model uses an inductive learning mechanism, it is completely independent of human judgments or ratings; there is no outside influence on the model's learning process. Additionally, it is impossible to introduce regularity via the model itself, as the language input to the model essentially *creates* the model itself through the global co-occurrence learning algorithm. The fact that the HAL output *has organization at all*, means that there was organization (i.e., statistical regularities) in the input.

Final corpus selection

A comparison of all possible sequences of lengths two to ten, to the number of actual sequences of lengths two to ten, was used to measure entropy. Low entropy (high organization) songs were characterized by having a small percent of the possible sequences present. The possible sequences were calculated, for comparison purposes, by randomizing the sequence order, keeping frequency consistent (Seitz, personal communication, 2010). The entropy analysis was conducted on the entirety of each of the four corpuses (full, wo62, wo96, wo62and96), plus each individual song in each of the following conditions: full, wo62split, wo62lumped, wo96split, wo96lumped, wo62and96split, wo62and96lumped. Split and lumped versions referred to alternate readings of the Ward's Cluster Analysis, which does not always provide an exact solution.

Graphs of the entropies at each sequence length for songs in the full corpus condition were compared (see Figure 9). This comparison showed that song62 was anomalous, having a very different structure than any of the other songs, namely an entropy that increased with sequences of length three to

"make," and therefore a higher proportion of the ones possible (represented by the random condition) would appear.

It was therefore determined that the wo62 corpus would be used for all further analysis. The split version of the corpus was used because it generally yielded lower entropies. The clustering pattern produced by this corpus yielded six Classes, which were regarded as grammatical and/or semantic classes and used to characterize patterns in the songs.

Confirmatory analysis

After the wo62 corpus was chosen, a split-half procedure using the "mixed" halves referred to above was completed in order to confirm reliability of the overall technique. Using Cohen's kappa (1960), each of the split halves was compared to the full corpus, and kappas of .4 and .5, respectively, were calculated. Comparison of the wo62 corpus to randomized versions of split1 and split2 yielded trivial kappa values of .01 and .1, respectively. This final comparison to a randomization of each of the splits was done

because there is no precedent for the use of Cohen's kappa in a situation like this. In clinical psychology, kappas of magnitude .4 and .5 would indicate "moderate" agreement (Cicchetti & Sparrow, 1981).

Are sequential patterns equal to grammatical patterns?

The human language system is composed of grammatical classes from which we are able to choose words to piece together sentences. For example, to create a basic sentence structured *subject + verb + direct object,* we are able to choose from a huge vocabulary of subjects, verbs, and direct objects; many of which are interchangeable. Consider, for example;

> Boy sees dog Boy sees cat Boy sees mouse Boy walks dog Girl sees dog

And so forth. Imagine you did not know what a dog, cat, or a mouse was. Given one sentence from the above set, you would have very little information. Given the first three, you would have more. Dog, cat, and mouse are contextually similar in that they are all things a boy can see, in addition to belonging to the class that is direct objects. Given all five sentences, you could then surmise that the act of seeing is not exclusive to the male gender, as the girl can also see the dog (and, therefore, she can most likely see the cat and mouse as well). In addition, you would learn that not only can the boy see the dog, he can also walk it – and therefore most likely the girl can as well. These inferences are all made possible by contextual similarities within the sentence.

To demonstrate the technique used in this study in a more familiar format, the Elman corpus discussed above was used. After classes were color coded and mapped onto the original corpus, it is possible to compare HAL's accuracy to the correct grammatical categories in human language – a luxury we do not have when dealing with animal vocalizations. HAL does fairly well; there is a noun cluster (purple) and a verb cluster (blue). HAL categorizes direct objects into two categories – pink and tan, with the pink cluster representing breakables (see Figure 10). The categorization is fairly comparable to the "correct" categorization of the three classes directly to the left (that, in and of itself, is not always exact – for example, the pattern is briefly interrupted at "cat eat mouse"

because "mouse" has received the overall classification of noun, not direct object). However, what if we did not know the words? In Figure 11 the words are removed and we just see patterns of color. These color patterns represent the patterns of grammatical classes that occur in our language. There is similar patterning throughout the humpback whale corpus. Because these patterns are based on classes distinguished by the HAL model, they are not recognizable simply by examining the order of the units. Likewise, the colored patterns from the Elman corpus come from the grammatical classes (whether they were created by HAL or by the experimenter's hand), not from the words themselves. The existence of

these patterns in humpback whale songs provides strong support for the hypothesis that the whales use global co-occurrence when creating their courtship songs.

Frequency Analysis

Initial analysis of the songs was accomplished by examining the frequency of occurrence of each of the classes. Because the number of songs available for comparison here is low, these results must be confirmed by additional analysis. In addition, the development of statistical techniques that could be used for a comparison across songs, despite the units being categorical data, is a necessity. Lastly, three classes – Class Green, Class Pink, and Class

Yellow – consist of one unit, that makes generalization beyond mere presence or absence impossible to justify. However, there are some conclusions about class frequency that can be supported.

Turks and Caicos have the most distinctive repertoire. Class Orange is almost completely unique to this region, and Class Pink and Class Dark Purple never appear there at all.

The Lesser Antilles songs seem to differ with the year of recording (and are generally regarded as different groups throughout this experiment). This is particularly apparent in the use of specific units from Class Dark Blue; while the overall usage of Class Dark Blue remains roughly the same over time, in 1973 the Class Dark Blue units that are used are nearly all units 20 and 21 (unit $20 = 10.0\%$, unit $21 = 12.3\%$, unit1 = 0%, unit12 = 1.1%). However, in 1976, this is completely reversed, and the composition of Class Dark Blue is almost entirely units 1 and 12 (unit $20 = 3.5\%$, unit $21 = 1.5\%$; unit $1 = 10.4\%$, unit $12 = 11.1\%$). If general meaning conveyed by Class Dark Blue remains the same, then it is not unrealistic to surmise that the dialect changed over this period of time from one set of units to the other, in a way similar to the introduction of new words to the human language that may be similar to ones already established. This finding may be support for the inherent substitutability of units within a particular class.

Lastly, the songs in Puerto Rico appear to be slightly more diverse than songs in other regions. In the other locations approximately 70 percent (TC = 72%, LA73 = 68%, LA76 = 70%) of all units can be accounted for by the two Classes that are also highest in frequency. However, in Puerto Rico, the top two frequency classes account for 61% of the units. This decrease in uniformity, although seemingly slight, will appear in other analyses as well.

Sequence Analysis

Some generalizations regarding the sequences can be made across all songs. It was very common for a song to consist of one or two "backbone" Classes, from which units occurred many times in a row (bearing in mind that although the units themselves might be different, the class is the same, so this backbone would not appear in a conditional probability analysis, where the units would simply appear as their identified selves). Within this backbone, single "drop in" units occurred at intervals that were too large and too variable for a sequential analysis to handle.

Differences in the composition of the backbone were evident, as were distinct patterns of classes within the songs. Songs had "roots," or sequences which appeared consistently. These roots were fairly consistent across all songs from a region, with the exception of songs from Puerto Rico. Using three unit

68

"roots," (as there were consistently more of these than any other length), Figure 12 shows the proportion of similar roots across songs.

What follows is a review of some of the more significant sequences found. Their implications and relationships to each other and across songs and regions will be discussed in the following sections.

Puerto Rico

Songs from Puerto Rico were the least uniform of the geographical locations. Song96 was particularly anomalous, being composed primarily of long strings of Class Pink (P) interrupted by units from Class Light Purple (LP), and shorter strings of Class Light Purple interrupted by units from Class Pink. Most likely this song should have been removed from the analysis at an earlier point; however, it was not identified as anomalous by the entropy analysis, potentially because it was disproportionate in terms of the frequency of a single unit as opposed to an entire Class. Further discussion of songs from Puerto Rico will exclude this song. However, it is important to note that the dissimilarity within the region's songs is not entirely due to Song96.

There was no clear backbone in the songs from Puerto Rico – song70 had a backbone of units from Class Light Blue (LB), song75 had a backbone of units from Class Light Purple, and song74 had a backbone composed of units from each. Song70 and song74 were most alike, sharing the root sequences LB+DB+LP and DB+LP+LB (see Figure 13), in addition to having units from Class Dark Blue (DB) nearly always occur as single units (i.e. there were very few examples of more than one unit from Class Dark Blue in a row). Song75 contained units from Class Yellow (Y) in its patterns, and these patterns appeared to be more complex variants (e.g. additional repeats) on the patterns appearing in the other two songs. In addition, the backbone in song75 was much more difficult to distinguish.

Turks and Caicos

Songs recorded at Turks and Caicos were far more consistent than songs recorded in other locations. All three songs showed a backbone of Class Orange (O), a Class almost exclusive to this region, with drop-ins from Class Light Purple (although the backbone was more mixed between these Classes in song119). In all cases, any sequence of a length of more than three units (with the exception of one sequence in one song) was composed entirely of units from Class Orange and Class Light Purple. In addition, in sequences longer than three to four units, units from Class Light Purple were generally only found singly. Only

in song119 were there a sufficient number of sequences with consecutive units from Class Light Purple to warrant mention.

Lesser Antilles

Songs recorded in the Lesser Antilles tended to share more characteristics when they were recorded in the same year; however, general trends across years were present as well. In 1973, the backbone of Lesser Antilles songs was from Class Light Purple; however, in 1976, the backbone was split between Class Light Purple and Class Light Blue. In 1973, the patterns for creating sequences were

straightforward. The non-backbone classes (Dark Blue, Dark Purple (DP), and Yellow) never co-occurred in the moving window; they only occurred in sequences with units from Class Light Purple, where they either alternated (i.e. DB+LP+DB+LP), or occurred in doubles (LP+DP+DP+LP or DP+LP+LP+DP). When these patterns occurred in the songs from 1976, they were less organized – for example, instead of simply two units in the middle of a sequence such as DP+LP+LP+DP, the number present was much more variable. More elaborate sequences were seemed to be present, such as DB+LB+G+LB+LB or LP+G+LP+LB; however, they could not be claimed to be entirely consistent as units would occasionally switch places or repeats would be added.

Entropy Analysis

Examining the results of the analysis of entropy (as defined by the number of sequences of a particular length in a song divided by the number of sequences of the same length when the units in that song are randomized) provided data that parallels the sequence analyses.

The entropy at each sequence length in a particular song can be graphed (Figure 14). Looking at these figures, the similarities and differences identified by the sequence analysis are evident.

In Puerto Rico (Figure 14a), the two most similar songs, song70 and song74 have very similar patterns of change in entropy over time, while song75, the more complex of the songs, occupies a different trace; it finishes with a higher entropy (less organization) than the other two. This is indicative of larger, less organized sequences at longer lengths, and is congruent with the addition of units from Class Yellow (which appears in song75 but not song70 or song74).

In Turks and Caicos (Figure 14b), there is a similar pattern. Although the songs in this region are generally more ordered, song102 and song118 are quite similar and their entropy graphs are indicative of this. Song119, as mentioned above, differs from the other two in that the backbone is less obvious and it is the only song in which multiple units from Class Light Purple could be found consecutively. Song119 has higher entropy at longer length sequences.

Finally, the entropy graphs for the Lesser Antilles (Figure 14c) are particularly interesting because they reflect the uniformity found within the sequence patterns. All four songs have very similar patterns of

entropy measurements, most likely owing to similar rules for sequence construction. Additionally, the two songs recorded in 1973 are represented by the two lowest traces and the two songs recorded in 1976 are the two highest traces. This parallels the conclusions drawn from the sequence data; the 1976 songs are less organized than the 1973 songs; they have variable numbers of repeated units, and thus higher entropy.

DISCUSSION

The HAL model is meant to measure global co-occurrence, the formation of cognitive representations by the use of context in language. The Classes identified by the analysis come directly from the whale song input. HAL requires no outside teacher and does not alter the input beyond summing and weighting co-occurrences, and adjusting for frequency of occurrence. The result is that there is no chance that the patterns found are artifacts of a computational process - the model is completely transparent. The Classes that were identified can be posited to be grammatical or semantic categories; if a pattern is found within a song that, for example, alternates between Class Yellow and Class Light Purple, it does not matter which units from within these Classes are used, as they all serve the same semantic or grammatical purpose. Just as English grammatical rules dictate the three classes "noun, verb, and direct object" to be ordered as such in a sentence, patterns found in humpback whale song may be obeying similar rules.

Frequency Analysis

Analysis of the frequency of occurrence of units in each cluster provides a basic description of songs in the three geographic areas.

Some Classes are almost entirely unique to a particular region, such as Class Orange is to Turks and Caicos. Monitoring the usage of Class Orange would be an excellent way to empirically test the transition of vocalizations between geographic areas, as its progress could be tracked into nearby geographical locations.

On the other hand, the Class usage in Puerto Rico appears to be more diverse, supporting the idea that the Puerto Rican songs are at least in part the product of convergence of the songs from neighboring areas.

Frequency also is a key factor in substitutability. If the Classes shown by the HAL model are the result of lexical co-occurrence, then the units in a particular Class should have some degree of basic substitutability. For example, just as different regions of the United States use the words "soda" and "pop" to refer to the same type of beverage, it is possible that in the Lesser Antilles in 1973 unit20 and unit21, the more frequent units in Class Dark Blue, were used to convey the meaning of that Class, while in 1976, unit1 and $unit12 - which became most the frequent units in these years - were used to convey the same$ meaning.

Sequence Analysis

One of the more important theoretical insights from HAL analysis has to do with the role of sequence. When unit identity is analyzed, for example in a conditional probability, the analysis, naturally, focuses on the unit. In human language, this is the equivalent of only being able to recognize "Boy sees cat" as a grammatical pattern if it is repeated over and over without variation. "Boy sees dog" or "Girl sees cat" would not be recognized as a correct grammatical pattern. The sequence analysis presented here was able to identify sequences at the Class level that were unique to both geographical regions (or, in the case of the Lesser Antilles, time), and to individual song. The specifics of the most consistent of these patterns have been discussed previously and are highlighted in Figure 15 (full corpuses can be found in Appendix B, while frequency counts can be found in appendix D).

PR 70	PR 70	PR 70	PR 75	TC 74	TC 74	TC 74	LA 73	LA 73	LA 76	LA 76
117770	117774	117775	128296	118102	118118	118119	110347	110858	118171	118172
pair13	uzit16	pair15	usit20	uzitó	sait12	paid3	poid 15	usi01	usid)	ne.it1
usid.	v cid 22	paid 10	unit25	usit11	paid 12	uzid3	paid19	paid3	pair10	paid 18
past 17	uzit16	paid24	unat24	uzato	uzató	man ²	uzit15	usit21	naill3	next1
usit22	usi02	nek20	usit20	naill	usit12	neid8	usii 15	neid S	paid 10	usit12
paint6	uzit16	usid4	$0 = 20$	mith	pair12	nait3	nait15	usit21	Beach	voir13
uzitl	uzit16	usi04	usid00	mid.	said:1	usid3	point 19	naidS	paid 10	nait?
uzit17	uzit16	paid 15	paid 0	unit5	mont	poid's	uzit)	usit21	poid 13	poid6
usi01	uzit17	paid 10	usit25	mait5	usi6	uzit9	našti 15	uzit3	pair10	naid 13
uzit17	usi02	nait18	unit20	mid	maith	uzit3	uzát13	usi01	nait13	usit1
uzit17	naith	unit19	usi 20	usit3	maith	mont	voit15	uzid3	paid 10	voir13
poid 17	unit)4	usidó	poid 19	poit5	usid3	usid3	paid9	0.621	poid 13	poid)
usi01	nait 17	uzató	paid 9	uaid3	uzit3	mont5	pair19	uzit3	pair10	usitl
uzit13	veit22	usitl	point19	mids	máS	uzit3	paid 19	usit21		
usii 17	uzit16	uzál 8	point19	usid3	maith	maith	paid19	usii 15	BEAT paid 10	BEAT neát I
nail 7	18.022	pairl0	point!9	mont	nait 11	uzi03	next ⁸	usi01	paid 3	nait 17
uzit16	uzit16	paid?	point19	poit5	voit5	poit5	nait 17	neid8	paid 10	naid 17
	naid			poit5				usit21		
nsid 17 nait 17	usi02	neát I naid 18	paid 19 poit19	mids	našti l monts	usid3 min	neit3 naid 17	usid9	usid I post10	neid S nait13
uzit16	uzit16	uzit10	unit19	unit3	voit)	uzit3	uzio	usit21	voir13	unit)
našt16	usi01	usitl	point19	poit5	nait 11	mids	usi01	usid9	point 10	nait13
pair16	paid 19	usi03	paid 19	usi6	usit12	usi6	paid3	usi01	nait13	nait13
uai:02	100022	uait10	unit19	mail	matto	uzit?	usi01	nait9	pair ₁₀	Bail
usii 17 uzit 17	uzit16 <u>usi02</u>	usitl uzit18	paid 19 unit19	usit10 maith	maid2 nait 11	uzit9 uzit3	usii 15 unit21	usi01 unit3	BEAT! BENT	usit9 BENT
uzitó	našt6	naid4	point19	usio	monts	uzit3	usi0	usi01	paid 10	nait9
usató	uzato	usitl	unit19	mont	uzato	paid 6	paid 1	voir15	paid.	uzatli
uaid)	naith	paid 18	unit19	uzit10	poit5	uzato.	unit19	DEAD	uzit9	Base
uzit13	usi04	neid4	point19	mits	maid2	uzitó	usi01	nait9	uzá3	uzit13
paid 16	usi01	poit14	poid 19	usi6	usit12	uzátó	paid3	paid?	pair10	paid 10
nasil 7	paid 7	BEAM	past19	maith	mont	18822	usi01	Bast9	used	BEATT
nait 17	usit21	voir18	poid19	neid8	mail)	usitó.	uzit9	usid9	neid3	usit 10
uzit17	nail9	paid 10	pain19	nait3	našti l	naid 13	usi01	pair15	nait 10	voir13
				poit5	poit5					
uzit16	point19	voit14	unit19			maid.	uzit3	uzit9	paid 3	mailS
uzit16	unit17	neid4	unil9	poid's	nait 11	uzit)	osi21	naits	uzál5	mail4
naill3	unit24	poid 14	post19	uaill0	naid3	18822	uzid9	usiO	nast3	paid 10
uzit16	neát1	next3	Bast 24	mait5	usit I I	usit11	usi01	usit10	usi6	v ai 23
voit16	usi03	paid 18	poid ₁₉	Bail	paid 10	poid 11	poid ₁₄	poid ₁₄	nait15	paid 10
past16	paint6	paid3	unit24	marto	paid 11	paid 6	next21	unit3	usid	BEATT
uzit16	usit12	paid 18	paid19	usi6	nait 11	12.822	mail	paid 10	naidS	uzit10
veit22	neátl	usi3	paid 19	mits	mon2	nait16	usi01	uzit9	nail9	uzát13
uzit16	$0 = 25$	poid ₁₄	paid 19	nait3	nait 11	unit16	poit?	paid 15	unit3	paid 10

Figure 15. Examples of sequences found. Note that sequences are made from Classes, and units within a Class may
vary.

unit ₁₇	unit3	unit12	unit ₁₅	unit7	unit ₁₀	unit3	unit ₃	unit ₃	unit ₁₉	unit9
unit ₁₇	unit ₁₀	unit12	unit ₁₉	unit7	units	unit9	unit ₃	unit ₁₄	unit ₂₄	unit ₈
unit ₁₇	unit ₁₃	unit ₁₁	unit ₁₉	unit7	units	unit5	unit ₂	unit4	unit4	unit ₂₃
unit ₁₇	unit4	unit ₁₈	unit ₁₅	unit9	unit2	unit ₈	unit ₁₉	unit ₁₄	unit ₁₅	unit4
unit3	unit ₂₃	unit ₃	unit ₁₉	unit ₂	unit3	unit2	unit ₃	unit4	unit4	unit ₂₃
unit ₈	unit4	unit9	unit ₁₅	unit5	unit3	unit5	unit3	unit ₁₄	unit ₂₅	unit6
unit1	unit ₂₃	unit3	unit ₁₉	unit ₂	unit ₈	unit6	unit9	unit4	unit ₁₉	unit ₈
unit ₂₂	unit4	unit9	unit ₁₉	unit5	unit4	unit8	unit ₈	unit ₁₄	unit ₁₉	unit7
unit ₁₆	unit ₂₂	unit9	unit20	unit5	unit ₂	unit6	unit3	unit4	unit ₂₃	unit ₈
unit ₁₇	unit ₂₃	unit ₁₆	unit ₁₅	unit3	unit5	unit5	unit14	unit ₁₄	unit4	unit9
unit ₁₃	unit4	unit ₁₂	unit ₁₉	unit5	unit ₁₀	unit6	unit4	unit4	unit9	unit ₈
unit ₁₇	unit3	unit ₁₂	unit ₁₉	unit6	unit2	unit2	unit14	unit ₁₄	unit9	unit20
unit ₁₇	unit ₂₃	unit21	unit ₁₅	unit5	unit5	unit ₁₁	unit3	unit4	unit ₂₅	unit3
unit7	unit4	unit ₁₈	unit ₁₉	unit6	unit2	unit7	unit ₁₄	unit ₁₄	unit24	unit ₁₅
unit ₁₇	unit ₂₁	unit ₃	unit ₁₅	unit6	unit ₁₀	unit ₁₁	unit3	unit4	unit3	unit3
unit ₁₆	unit4	unit ₁₅	unit ₁₉	unit6	unit ₈	unit7	unit ₁₄	unit ₁₄	unit9	unit20
unit ₁₇	unit ₂₂	unit ₂	unit ₁₅	unit6	unit ₁₀	unit ₁₂	unit ₃	unit4	unit4	unit ₈
unit ₁₃	unit ₂₃	unit ₁₅	unit ₁₉	unit6	unit2	unit9	unit9	unit ₁₄	unit ₂₅	unit ₈
unit7	unit4	unit9	unit9	unit6	unit5	unit ₁₂	unit9	unit ₃	unit25	unit ₁₀
unit ₂₂	unit ₁₄	unit ₁₁	unit ₁₅	unit6	unit2	unit9	unit ₈	unit3	unit ₂₄	unit ₈
unit ₂₁	unit3	unit ₁₆	unit ₁₉	unit6	unit5	unit ₁₁	unit ₃	unit ₁₄	unit ₃	unit ₁₅

Using the color coding technique developed here, the sentences "Boy sees cat," "Boy sees dog," and "Girl sees cat" would all be identified as grammatically and semantically similar; "boy" and "girl," being nouns, would belong to one Class and would be identified with the same color; "sees", a verb, would be a different color; and "cat" and "dog," both direct objects in this case, would be a third color – creating an identifiable pattern. That said, there are still variations in contextual usage and it is speculated that meaning differences would still be important within Classes.

It is important to note, when reviewing Figure 15, that some of the assertions in the results section may appear to be untrue. For example, it is discussed that no more than three or four units from Class Light Purple ever appeared consecutively in song102 or song118. Yet there is clearly a sequence of six units from Class Light Purple in song118. This contradiction is due to the fact that only sequences that occurred more than five times within a song were considered in the analysis. Therefore, although it may seem that the general rules for sequences identified via the entropy analysis are violated in the example provided, it is important to remember that the exceptions in this example are unique or rare occurrences.

Puerto Rico

Songs recorded in Puerto Rico were the least uniform of the three regions. Song96 was particularly anomalous – it was notably shorter and contained long repetitions of Class Pink, a class consisting of one unit and found infrequently in other songs. As a result, it was generally excluded from the analysis, although it should be noted that the variation within the Puerto Rican songs was not entirely due to song96.

Song "backbones" in Puerto Rico were either composed of units from Class Light Blue, Class Light Purple, or both. However, in all cases it is important to note the diversity of units here – because these backbones are composed of different units from the same Class, they could only be distinguished by an analysis of global co-occurrence. Geographically, Puerto Rico is located between Turks and Caicos (to the north) and the Lesser Antilles (to the south). As a result, if song elements were passed between whales (and populations) over geographic regions, it is plausible that songs recorded in a central area would be a mixture. For example, song70 and song74 both display elements common to song171 (recorded in the Lesser Antilles) - a backbone of units from Class Light Blue and Class Light Purple; "drop in" units from Class Light Blue, Class Light Purple, and Class Dark Blue; and root patterns composed of units from these Classes.

Turks and Caicos

Songs from Turks and Caicos were categorized by both their consistency and the presence of Class Orange, which was almost exclusively unique to this region (the highest occurrence in any other song was 1.6%, and in any other song it appeared in its frequency was less than 1%). For all intents and purposes, any sequence of more than three to four units in the Turks and Caicos was composed solely of units from Class Orange and Class Purple. In addition, longer sequences saw units from Class Purple only in single occurrences. Units from other Classes were recorded in Turks and Caicos, but only in shorter sequences. This lack of diversity may be evidence of a smaller "vocabulary" in the Turks and Caicos region; Class Orange is composed of only two units, and although all of the units from Class Purple appear

at some time in the region, there was a distinct bias towards unit3, unit8, unit9, unit10, and unit11. Out of the nine units in Class Light Purple, these five accounted for 95.4% of the occurrences of the Class in the Turks and Caicos. This effectively created a vocabulary of seven units with which to build sequences of song at length greater than three to four units in this geographic region. For purposes of comparison, the song with the next smallest vocabulary was song74, which had 16 units and the only potential bias being towards unit16 and unit22 (Class Light Blue) - two units representing 75% of the occurrences of their five unit Class. A smaller vocabulary creates less lexical and/or semantic flexibility and thus less diverse songs. With this knowledge, one might hypothesize that this population of whales is relatively new and/or fairly isolated, which would consequently slow the process of change in song. Thinking back to the diversity of songs in Puerto Rico, a scenario such as a new or isolated population in the Turks and Caicos might explain why there appears to be very little similarity between the songs from these two regions, relative to the similarity between the songs of Puerto Rico and the Lesser Antilles.

Lesser Antilles

Songs in the Lesser Antilles appeared to get more complex over time. Over the course of the three years between sets of recordings, the backbone of the songs changed from exclusively Class Light Purple to a combination of Class Light Blue and Class Light Purple. In addition, the root patterns became more complex and sometimes even unpredictable. It is possible that there is a pattern of divergence here. The songs recorded in 1973 show similarity in pattern, containing root patterns that alternate Classes in a x+y+x+y or x+y+y+x pattern. In 1976 the songs change more. As previously mentioned, song171 is similar to some of the songs recorded in Puerto Rico, as if the whale(s) singing this song influenced or was influenced by singers in this region. Song172 becomes much more diverse and much less predictable; almost as if a new song or variation thereof were in the process of being created.

Entropy Analysis

The proposed ideas from the sequence data are supported in the overall entropy analysis. The variation in the Puerto Rican songs is evident; they show no agreement on the sequence length at which organization is the highest (song70 – eight units, song74 – seven units, song75 – six units). In the entropy graphs of the Lesser Antilles, one would expect that if singers in the Lesser Antilles are branching out over time, the songs recorded in 1976 would have more entropy than those recorded in 1973 (which is true). In Turks and Caicos, one needs to bear in mind that the strong decrease in the number of Classes used to create sequences occurred at sequences longer than three to four units. At five units, the decrease in the number of units causes increased predictability (decreased entropy). However, entropy increases from this point on. Just as prediction is a moot point when a series is random, so is it when a series is too repetitive; and even more so when the series is repetitive with one insertion at random intervals, as becomes the case in longer sequences in the Turks and Caicos due to the backbone and drop-in units.

It is vital that, while considering the ideas in this discussion, that one keep in mind the small sample size involved in this analysis. Although the actual songs contained large numbers of units, the number of Classes is relatively small, and several Classes only contain one unit. In addition, although the region comparison provides intriguing avenues to investigate, a sample size of two to four songs per region and/or year is far too small to draw firm conclusions. However, the results and ideas presented here are intriguing and should serve as a foundation for continued discussion and experimentation.

REFERENCES:

- Baker, M. C., & Gammon, D. E. (2008). Vocal memes in natural populations of chickadees: why do somememes persist and others go extinct. *Animal Behaviour, 75*(1), 279-289.
- Baron, S. C., Martinez, A., Garrison, L. P., & Keith, E. O. (2008). Differences in acoustic signals from Delphinids in the western North Atlantic and northern Gulf of Mexico. *Marine Mammal Science, 24*(1), 42-56. doi: doi:10.1111/j.1748-7692.2007.00168.x
- Berchok, C. L., Bradley, D. L., & Gabrielson, T. B. (2006). St. Lawrence blue whale vocalizations revisited: Characterization of calls detected from 1998 to 2001. *The Journal of the Acoustical Society of America, 120*(4), 2340-2354.
- Bogdan, R. C., & Biklen, S. K. (1998). *Qualitative research for education: An introduction to theory and methods*. Boston: Allyn and Bacon.
- Burgess, C., & Lund, K., (2000). The dynamics of meaning in memory. In E. Dietrich and A.B. Markman
- (Eds.), *Conceptual and representational change in humans and machines* (pp. 117-156). Mahwah, New Jersey: Lawrence Erlbaum Associates.
- Caldwell, M. C., & Caldwell, D. K. (1965). Individualized Whistle Contours in Bottle-nosed Dolphins (Tursiops truncatus). *Nature, 207*, 434-435.
- Chu, K. (1988). Dive times and ventilation patterns of singing humpback whales (Megaptera novaeangliae). *Canadian Journal of Zoology, 66*, 1322-1327.
- Cicchetti, D. V., & Sparrow, S. S. (1981). Developing criteria for establishing interrater reliability of specific items: Applications to assessment of adaptive behavior. *American Journal of Mental Deficiency, 86*, 127-137.
- Clapham, P. (2000). The humpback whale: Seasonal feeding and breeding in a baleen whale. In J. Mann, R. Connor, P. Tyack & H. Whitehead (Eds.), *Cetacean societies: Field studies of dolphins and whales* (pp. 173-196). Chicago: University of Chicago Press.
- Cohen, J. (1960). A Coefficient of Agreement for Nominal Scales. *Educational and Psychological Measurement, 20*(1), 37-46.
- Darling, J. D. (1983). *Migrations, abundance and behaviour of 'Haiwaiian' humpback whales (Megaptera novaeangliae).* PhD, University of California, Santz Cruz, Santa Cruz.
- Darling, J. D., Jones, M. E., & Nicklin, C. P. (2006). Humpback whale songs: Do they organize males during the breeding season? *Behaviour, 143*(9), 1051-1101.
- de la Torre, S., & Snowden, C. T. (2009). Dialects in pygmy marmosets? Population variation in call structure. *American Journal of Primatology, 71*(4), 333-342.
- Deecke, V. B. (2006). Studying Marine Mammal Cognition in the Wild: A Review of Four Decades of Playback Experiments. *Aquatic Mammals, 32*, 461-482.
- Deecke, V. B., Ford, J. K. B., & Spong, P. (1999). Quantifying complex patterns of bioacoustic variation: Use of a neural network to compare killer whale (Orcinus orca) dialects. *Journal of the Acoustical Society of America, 105*(4), 2499-2507.
- Delarue, J., Todd, S. K., Parijs, S. M. V., & Di Iorio, L. (2009). Geographic variation in Northwest Atlantic fin whale (Balaenoptera physalus) song: Implications for stock structure assessment. *The Journal of the Acoustical Society of America, 125*(3), 1774-1782.
- Eliades, S. J., & Wang, X. (2008). Neural substrates of vocalization feedback monitoring in primate auditory cortex. *Nature, 453*, 1102-1106.
- Elman, J. L. (1990). Finding structure in time. *Cognitive Science, 14*, 179-211.
- Frantzis, A., & Alexiadou, P. (2008). Male sperm whale (Physeter macrocephalus) coda production and coda-type usage depend on the presence of conspecifics and the behavioural context. *Canadian Journal of Zoology, 86*(1), 62-75.
- Frazer, L. N., & Mercado, E. (2000). A sonar model for humpback whale song. *IEEE Journal of Oceanic Engineering, 25*, 160-182.
- Gallistel, C. R., & Gelman, R. (2000). Non-verbal numerical cognition: from reals to integers. *Trends in Cognitive Sciences, 4*(2), 59-65.
- Green, S. R., Mercado, E., Pack, A. A., & Herman, L. M. (2007). Characterizing patterns within humpback whale (Megaptera novaeangliae) songs *Aquatic Mammals, 33*(2), 202-213.
- Handel, S., Todd, S. K., & Zoidis, A. M. (2009). Rhythmic structure in humpback whale (Megaptera novaeangliae) songs: Preliminary implications for song production and perception. *The Journal of the Acoustical Society of America, 125*(6), EL225-EL230.
- Kirschel, A. N. G., Earl, D. A., Yao, Y., Escobar, I. A., Vilches, E., Vallejo, E. E., et al. (2009). Using Songs To Identify Individual Mexican Antthrush Formicarius moniliger: Comparison of Four Classification Methods. *Bioacoustics, 19*(1-2), 1-20.
- Kohonen, T. (1982). Self-organized formation of topologically correct feature maps. *Biological Cybernetics*, *43*, 59-69.
- Lund, K., & Burgess, C. (1996). Producing high-dimensional semantic spaces from lexical co-occurrence. *Behavior Research Methods, Instruments, & Computers, 28*(2), 203-208.
- Mellinger, D. K. (2008). A neural network for classifying clicks of Blainville's beaked whales (Mesoplodon densirostris). *Canadian Acoustics, 36*(1), 55-59.
- Miksis-Olds, J. L., Buck, J. R., Noad, M. J., Cato, D. H., & Stokes, M. D. (2008). Information theory analysis of Australian humpback whale song. *The Journal of the Acoustical Society of America, 124*(4), 2385-2393.
- Miller, G. A. (1956). The Magical Number Seven, Plus or Minus Two: Some Limits on our Capacity for Processing Information. *Psychological Review, 63*, 81-97.
- Parsons, E. C. M., Wright, A. J., & Gore, M. A. (2008). The nature of humpback whale (Megaptera novaeangliae) song. *Journal of Marine Animals and their Ecology, 1*(1), 22-31.
- Payne, R., & McVay, S. (1971). Songs of humpback whales. *Science, 173*, 583-597.
- Placer, J., Slobodchikoff, C. N., Burns, J., Placer, J., & Middleton, R. (2006). Using self-organizing maps to recognize acoustic units associated with information content in animal vocalizations. *The Journal of the Acoustical Society of America, 119*(5), 3140-3146.
- Pond, R. L., Darre, M. J., Scheifele, P. M., & Browning, D. G. (2010). Characterization of equine vocalization. *Journal of Veterinary Behavior, 5*(1), 7-12.
- Rendell, L. E., & Whitehead, H. (2001). Culture in whales and dolphins. *Behavioral and Brain Sciences, 24*(2), 309-+.
- Rickwood, P., & Taylor, A. (2008). Methods for automatically analyzing humpback song units. *The Journal of the Acoustical Society of America, 123*(3), 1763-1772.
- Riesch, R., Ford, J. K. B., & Thomsen, F. (2006). Stability and group specificity of stereotyped whistles in resident killer whales, Orcinus orca, off British Columbia. *Animal Behavior*.
- Riesch, R., Ford, J. K. B., & Thomsen, F. (2008). Whistle sequences in wild killer whales (Orcinus orca). *The Journal of the Acoustical Society of America, 124*(3), 1822-1829.
- Selin, A., Turunen, J., & Tanttu, J. T. (2006). Bird sound classification and recognition using wavelets. *Advances in Bioacoustics 2, 47*(3), 185-204.
- Smith, J. N., Goldizen, A. W., Dunlop, R. A., & Noad, M. J. (2008). Songs of male humpback whales, Megaptera novaeangliae, are involved in intersexual interactions. *Animal Behavior, 76*(2), 467- 477.
- Stafford, K. M., Moore, S. E., Laidre, K. L., & Heide-Jorgensen, M. P. (2008). Bowhead whale springtime song off West Greenland. *The Journal of the Acoustical Society of America, 124*(5), 3315--3323.
- Suzuki, R., Buck, J. R., & Tyack, P. L. (2006). Information entropy of humpback whale songs. *The Journal of the Acoustical Society of America, 119*(3), 1849--1866.
- van der Schaar, M., Delory, E., Catala, A., & Andre, M. (2007). Neural network-based sperm whale click classification. *Journal of the Marine Biological Association of the UK, 87*(01), 35-38.
- Watkins, W. A., Tyack, P., & Moore, K. E. (1987). The 20-Hz signals of finback whales (Balaenoptera physalus). *Journal of the Acoustical Society of America, 82*, 1901-1912.
- Weiss, B. M., Symonds, H., Spong, P., & Ladich, F. (2007). Intra- and intergroup vocal behavior in resident killer whales, Orcinus orca. *The Journal of the Acoustical Society of America, 122*(6), 3710-3716.
- Winn, H. E., Thompson, T. J., Cummings, W. C., Hain, J., Hudnall, J., Hays, H., et al. (1981). Song of the humpback whale - Population comparisons. *Behavioral Ecology and Sociobiology, 8*, 41-46.

Winn, H. E., & Winn, L. K. (1978). The song of the humpback whale (Megaptera novaeangliae) in the west indies. *Marine Biology, 47*, 97-114.

CHAPTER 4: MICE

INTRODUCTION

When Holy and Guo first published on the courtship vocalizations of male mice, they thought they were unique in deeming these ultrasonic vocalizations "songs" and identifying structural and temporal regularities (Holy $& Guo, 2005$). As they soon became aware, studies from as early as 1857 existed detailing audible courtship songs from mice (Guo $\&$ Holy, 2007); however, in combination with recent advances in genetic modeling of language disorders, this information was now a powerful new research technique.

Calls in several of strains of mice have been linked to specific behaviors, many of which facilitate the sequence of actions involved in courtship (Bartholemy, Gourbal, Gabrion, & Petit, 2004; White, Prasad, Barfield, & Nyby, 1998). For example, after pairing, the male mouse begins vocalizing with great intensity; continuing to do so throughout the series of sexual behaviors, and only ceasing (or severely decreasing his rate of) singing when engaged in tasks other than sniffing or mounting the female (Nyby, 1983). The feeling is mutual - playback experiments show that the ultrasonic songs produced by these males are excellent at attracting the attention of female mice – even as compared to artificial songs or the cries of pups. Furthermore, although desensitization is more rapid than might be expected, and the female's interest is independent of her reproductive state (Hammerschmidt, Radyushkin, Ehrenreich, & Fischer, 2009). Curiously, although female mice may be interested in the songs of males regardless of their own reproductive state, male mice are more selective - they produce songs only in response to urine scent from reproductive female mice, as opposed to other males or from sexually immature females (Pomerantz, Nunez, & Bean, 1983). They also respond at higher rates to the scents of novel females (as do females respond at a higher rate to the songs of novel males) (Musolf, Hoffmann, & Penn, 2010). Taken together, this appears to be strong evidence that songs are not only a key part in mating, but in sexual selection as well (Holy & Guo, 2005; Musolf et al., 2010; Pomerantz et al., 1983). The idea of a direct relationship to of mouse song to sexual selection is in turn compatible with the idea of analogous evolution of the use of

ultrasonic songs for courtship in a variety of species. This is indeed the case for bats (e.g. Bohn, Schmidt-French, Ma, & Pollak, 2008), cetaceans (Lammers, Au, & Herzing, 2003; Madsen & Wahlberg, 2007), several species of rodent (Kapusta & Sales, 2009; Toro & Trobalon, 2005; Wohr & Schwarting, 2007), at least one species of amphibian - the concave-eared torrent frog (*Amolops tormotus*; Feng et al., 2006), and at least nine different species of moths (Nakano et al., 2009). It is hypothesized that this type of communication has evolved at least in part as a result of noisy environments (Feng et al., 2006; Tyack, 2008) and that it is advantageous because it can be heard by the intended recipient, who would be located nearby, and not by those who it is not intended for, such as predators or rivals (Nakano et al., 2009). As the previous species list is extremely diverse, it can only be proposed that ultrasonic courtship songs such as these evolved analogously, and therefore the evolutionary pressures that are (were) conducive to this would be useful to study.

It has been suggested that vocalizations (and their unique variants) can be used for behavioral analysis, such as identifying the phenotype of a genetic condition (Scattoni, Crawley, & Ricceri, 2009). In fact, mouse models exist for several disorders involving communication, including Down Syndrome, Rett Syndrome, and social aspects of schizophrenia (Holtzman et al., 1996; Picker, Yang, Ricceri, & Berger-Sweeney, 2006; Scearce-Levie et al., 2007). This experiment focuses on another mouse model, the *Fmr1* knockout mouse (henceforth, KO mice), that is used as a model for fragile X syndrome (The Dutch-Belgian Fragile X Consortium, 1994). People with fragile X syndrome experience a range of symptoms dealing with cognitive and social impairment; included in this spectrum are linguistic deficiencies, however, the exact nature of their cause remains under debate (Abbeduto & Hagerman, 1997; Roberts, Price, et al., 2007). Sudhalter and colleagues tested males with linguistic deficits due to fragile X syndrome with two hypotheses in mind; that the deficit was due to deficiencies in syntactic abilities, that in turn caused characteristic repetitious speech, and/or that linguistic problems were due to difficulties with what they called "expressive semantic competence," which they defined as "the ability to choose the correct word from one's mental lexicon so as to produce a meaningful and well-formed thought" (1992, p. 66). They found the latter to be the case – showing more semantic errors in fragile X children than normal four year

old children, in addition to more semantic errors in sentences without contextual constraint than in those with. They further attributed the redundant speech of fragile X children not to syntax, but to the use of "placeholders" while attempting to recall the correct words, and believe the linguistic deficit in fragile X children is not one of word identification, but rather word expression (Sudhalter et al., 1992). However, many have questioned some of the methodologies of this study, and more recent studies have supported an approach that identifies syntactic abilities as the main root of language deficiency in fragile X syndrome (Price et al., 2008; Roberts, Hennon et al., 2007).

Similarities in both pitch and pattern have been found between the unusual cries of autistic infants and autistic model mice pups, that support the use and generalizability of mice as a model system for autism related disorders such as fragile X in humans. Even more specific to the construct of communication, there is strong evidence that the ultrasonic vocalizations of mice may be an appropriate parallel system to study vocal impairments in humans. Mice contain an analog to the human FOXP2 gene, often called the "language gene" (Lai, Fisher, Hurst, Vargha-Khadem, & Monaco, 2001), that, when tampered with, causes deficits in vocalization. Using recombinant technology, researchers have been able to re-create a human mutation in the mouse gene and then "knock-in" the gene, thus developing a mouse model of the human mutation. In a heterozygous mouse (one with only one copy of the knock-in gene), impairments were less severe than in a homozygous mouse (one with two copies of the gene), showing a direct correspondence between the gene and the impairment (Fujita et al., 2008). In addition, there is also an analog of FOXP2 in songbirds. Male zebra finches have two types of singing behavior linked to the FOXP2 gene – one in which song is directed toward females and one in which it is not (Jarvis, Scharff, Grossman, Ramos, & Nottebohm, 1998; Zann, 1996). Curiously, male mice with the vocalization difficulties inherent in the *Fmr1* model also display these patterns; their song appears much more scattered – sometimes directed at females and sometimes directed elsewhere (Rotschafer, personal communication). It is not unimaginable to hypothesize a sort of three way interaction between the communication and behavioral deficits evident in the fragile X model mice and mutations in both *Fmr1* and FOXP2; indeed, Holy and Guo (2005), in the paper originally characterizing ultrasonic songs in mice, speculate just this.

87

It has already been observed that KO mice vocalize differently than their "normal" or wild type (WT) conspecifics (Rotschafer, in preparation), and the main goal of this experiment was to establish whether the difference in communication is semantic (in which case the HAL model would show contextual differences in the usage of individual sounds by the two strains), or syntactic (in which case either the differences in vocalizations would stem more from the sequential acoustic make up of the sounds or there would be no common syntax at all; both cases in which the HAL clusters would not reflect any pattern of co-occurrence). Because recent research shows that, in terms of the expression of language deficits, fragile X syndrome and autism are comparable (Kover & Abbeduto, 2010), and because of the high degree of comorbidity between fragile X and Autism Spectrum Disorders (Abbeduto, Brady, & Kover, 2007), this information has potential to provide important insight into the types of communication deficits present in several severe disorders.

The study presented here examines two components of communication – syntax, or sentence structure (represented here as patterning), and semantics, or word meaning (represented here as global cooccurrence). To enable this to happen, two different perspectives were taken for comparison of the corpuses. In order to compare the syntax of the WT and KO corpuses, it was necessary to assume that the Classes identified in the HAL analysis of the WT corpus were "correct," and could therefore be mapped on to the calls produced by the KO mice. This would essentially result in a simulation of what the KO corpuses would look like if these mice understood the meaning of the calls they used (and therefore used them in the correct contextual relationships). With this assumption (done with the understanding that it is, to some degree, a leap of faith), it is possible to examine how the KO mice put together patterns – i.e., construct syntax. For example, this would be similar to a case in which despite understanding the words boy, ball, girl, tossed, threw, football; sentences such as "The football threw the boy" and "The ball tossed the girl" would be constructed. In this example, ball and football, and boy and girl, share global cooccurrences, however, the nouns and direct objects in the sentences – i.e. the syntax – are incorrect. Second, the Classes created by the KO corpus itself were examined as if they were unique to the KO corpus. This comparison essentially checks semantics; as the patterns (or syntax) are held constant and the

Classes (meaning or semantics) used to create the patterns are evaluated. For example, this would be similar to comparing two romance languages – the general sentence structure remains the same while the meaning changes between the two languages.

METHODS

Mouse songs were recorded between April 25, 2008 and June 5, 2009 in the lab of Khaleel Razak at the University of California, Riverside. Male mice were placed in a container accompanied by a female mouse and recordings were made of ultrasonic vocalizations until either a) the female allowed the male to mount, or b) the female was inattentive to the male for periods long enough to be deemed unreceptive by the experimenter. Songs were recorded with a Petersson D 1000X Ultrasonic Detector. For more information on the recording process, see Rotschafer (in preparation).

Two strains of mouse were used in this experiment. A control, or wild type (WT) mouse, and a genetically altered mouse, the *Fmr1* knockout (KO). The *Fmr1* knockout mouse is a model for Fragile X syndrome in humans (The Dutch-Belgian Fragile X Consortium, 1994), a disorder consisting of autism like social impairment and mental disability due to insufficient or complete lack of production of the FMR protein (Sutcliffe et al., 1992).

After collection, vocalizations were digitized and classified by hand according to visual inspection of their spectrograms; a classification method that, though time consuming and labor intensive, has been shown to be quite robust (Deecke & Janik, 2006; Janik, 1999). The classification was actually conducted as a part of an experimental procedure, however the goal of the classification in both experiments was identical (Trujillo, in preparation). A total of 23 call types were classified, although one type was a "noise" category (ambient sounds such as doors opening and footsteps), and one occurred so infrequently that it did not appear in the analysis. In total, calls from 13 WT mice and 30 KO mice were recorded (although later in the analysis, when the songs of individual mice were being compared, several mice with extremely short

songs (less than 20 calls) were dropped, effectively making this number 12 and 24, respectively, during that portion of the analysis). Songs sung by WT mice were significantly longer than those sung by KO mice, so the difference in quantity of songs was balanced by the length of songs in the two overall corpuses. Full corpuses can be found in Appendix C and frequencies can be found in Appendix D.

As discussed in the general methods, mouse songs were concatenated according to condition (WT or KO) and matrices were built using the HAL model. A variety of model parameters were used, including an unlimited matrix (almost no clustering), limits of 150 and 75, and window sizes of 10, 5, and 2. Using the split half comparison described in the humpback whale methodology, a limit of 150 and a window size of 2 were found to be the most robust when comparisons were made between whole and split corpuses $(WTK_{split1, split2} = .71, .94; KOK_{split1, split2} = .85, .89). Additional happens between outcomes of different$ parameter settings were calculated and can be found in Figure 16. These ranged from fair to moderate agreement, and while the agreement here may be less than that of the final corpus and its split halves, it is still substantially higher than a randomization such as that found in the humpback whale experiment, in which kappas were equal to .1 and .01. Frequencies of calls occurrence in the corpuses was positively correlated at $r = .853$ ($p \le .01$), so frequency did not play a part in experimental outcomes.

Corpus 1	Corpus 2	Kappa		
WT lim75w10	WT lim150w10	.48		
WTlim75w2	WT split1lim30w10	.25		
WTsplit1lim30w2	WTsplit1 lim75w10	.48		
KOlim75w2	KOsplit1lim75w2	34		
KOlim150w10	KOlim75w10	.22		
KOsplit1lim30w2	KOsplit1lim30w2	.28		

Figure 16. Calculated kappas for comparison between models with different parameter settings.

RESULTS

The final clustering (Class) patterns for the WT and KO mice can be found in Figure 17. In these diagrams vertical rows represent clusters output by the Ward's cluster analysis, while colors represent final mouse call Classes. In the case of each of the KO and WT condition, the top diagrams represent the final corpus parameters used in the experimental manipulations. However, as previously mentioned, multiple sets of parameters were tested, and several are also exemplified in the figure, below their respective final

corpuses. In some cases, these tests had bearing on the final classification. For example, although the final corpus parameters chosen (limit 150 and window size 2) were deemed to be most appropriate overall, it was also the case with these parameters that Class Yellow (calls 1, 4, 5, and 9) in the WT corpus was divided into two output clusters in the Wards Analysis (hence two vertical rows in the diagram). Therefore, experience with testing at other parameters, in which these four calls nearly always occurred together, justified their grouping into one Class. Calls clustered

differently for WT and KO mice. Cluster membership was almost completely altered between the two strains of mouse.

Manipulation 1: Checking syntax

WT Classes, if considered to be valid and reliably mapped onto the KO corpus, were completely distributed among the KO clusters. However, frequency of occurrence of each Class remained nearly the same between the two strains of mice (see Figure 18), with the only exceptions being Class Orange and Class Green.

Patterns also remained approximately the same, as judged by the length of uninterrupted stretches of the Class Yellow "backbone." The mean number of sequential calls from Class Yellow (i.e. number of calls in a row from Class Yellow before a call from another Class was "dropped in") in the WT corpus was 4.46 ($SD = 4.2$) and in the KO corpus was 4.81 ($SD = 3.69$). While the standard deviations on these averages may be very large, the two distributions overlap considerably, $(t(1172) = 1.96, n.s.$ p is greater than .05). For samples of the corpuses, both mapped with the Classes as established via the WT clusters, see Figure 19.

Class Orange (in WT mice) and Class Green (in KO mice) were anomalous in that they each appeared to be found almost entirely in their respective strains of mouse. Possible reasons for this will be explored later.

Manipulation 2: Checking semantics

As can be seen in Figure 17, when calculated independently in their separate corpuses, the resulting Classes in WT and KO strains of mice appear to be quite different. However, when the KO Classes were mapped back on to the KO corpus, it is initially evident that – as would be expected after the result of Manipulation 1 – patterns (or syntax) do exist. Once again, using the WT Classes as a standard for comparison purposes, the patterns can be assessed.

The Class Yellow backbone evident in the WT corpus is replaced by two classes – Class Light Blue and Class Pink. Specifically, where Class Yellow comprises from 47-89% of calls in each of the 12 songs in the WT corpus (beyond one exception, at 36%), the combination of Class Light Blue and Class Pink accounts for a slightly higher percentage of the KO corpus - 63-100% of calls in each of 23 songs (with 3 exceptions, two at 42%, and one at 47%). Mean length of uninterrupted sequences of Class Light Blue and Class Pink were 3.18 (SD = 1.64), and 3.70 (SD = 2.32), respectively. Again, while the standard deviations here are extremely high, the populations are shown to overlap significantly $(t(974) = n.s., p$ is greater than .05).

With respect to the specific order of Classes, it appeared as though the KO Classes were "trying" to maintain the patterned syntax established by the WT Classes. The pattern seemed similar; however the Classes that made up the patterns were not; meaning call order was similar, however, Classes were not. There was no one to one correspondence. For example, Figure 20ashows a comparison of two segments of KO mouse song coded twice - once with the KO Classes and once with the WT Classes. The WT Classes again show the Class Yellow backbone and drop ins, and there are some similarities in the patterns created by the KO Classes. However, the KO patterns are not a complete match for the correct WT patterns, as the individual units in semantic classes do not match. As shown in Figure 20b, for example, the calls in WT Class Dark Blue fall into a variety of Classes in the KO corpus; although they seem to do so in pairs, almost as if the KO mice were "trying" to keep the calls grouped together.

DISCUSSION

Manipulation 1

The WT and KO corpuses appeared similar when they were both mapped with the Classes from the WT corpus. This may be primarily due to the frequency of the four calls that composed the Class Yellow backbone, which was disproportionately high in both corpuses. The HAL model was run with a

limit that controlled for this high frequency when creating the Classes; however, the effect is circular. Because there are such a high number of calls 1, 4, 5, and 9, there is a high probability that any one of these calls will be followed by another in the group. When strings of just these four calls become longer than a plausible window size (i.e. longer than one would expect from a mouse, even considering a global contextual scheme), co-occurrence vectors for each of the calls will, very often, consist solely of the other three calls. As HAL creates representations (whose relationships can then be visualized as clusters) strictly

from these co-occurrence vectors, these calls are, in turn, are grouped in the same cluster.

This means that despite the fact that the KO corpus does not identify the same patterns of co-occurrence as the WT corpus – remember that calls 1, 4, 5 and 9 are NOT in the same cluster in the KO cluster analysis – the KO mice still manage to create some of the same syntactic structure using individual units (recall Figure 19). To put it another way, while the WT mice may be building the "backbone" of their songs with any one of the four calls in Class Yellow, the KO mice may be building the backbone of their songs by putting together combinations of call1, call4, call5, and call9. It is the difference between a "choose one of" type instruction and an "or... or... or" type of instruction. In essence, the KO mice can create the correct syntax; however they are not doing

so by using any sort of global semantic system.

Lastly, this particular mapping shows large amounts of Class Orange in particular songs – those sung by WT mice 26, 27, 35, and 36, and those sung by KO mice 31, 32, and 33 – and nearly none in other songs. Further investigation into the cause of this anomaly is warranted; if these recordings and/or

hnique been g this will or future this is not bther y which ons may itted must gated. on include onducive Γ in a n, rather ultural dialects that have

been evidenced in a variety of other species (Baker & Gammon, 2008; de la Torre & Snowden, 2009; Deecke, Ford, & Spong, 2000; Fehér, Wang, Saar, Mitra, & Tchernichovski, 2009; Putland, Nicholls, Noad, & Goldizen, 2006; Rendell & Whitehead, 2001; Wright, Dahlin, & Salinas-Melgoza, 2008), or transmission of vocalizations via learning or tutoring as has been shown in birds and is speculated upon by Holy and Guo (2005) (Beecher, Burt, O'Loghlen, Templeton, & Campbell, 2007; Belzner, Voigt, Catchpole, & Leitner, 2009; Nelson & Poesel, 2009; Pepperberg, 1994; Wheelwright et al., 2008).

Manipulation 2

Manipulation two was intended to check for semantics while maintaining a constant syntax between the corpuses. As previously noted, the Classes created by co-occurrence of calls in the KO corpus are quite different than the Classes that exist in the WT corpus. However, referring to Figure 20, rudimentary patterns of syntax are in evidence. Instead of one backbone Class, the KO mice appear to be using both Class Light Blue and Class Pink to comprise the backbone of their songs. In 14 out of 23 of these cases, the proportion of calls from Class Light Blue and Class Pink is approximately equal; the number of calls from each of the Classes was within ± 10 percent of the midpoint of their sum (for example, in KO Mouse #1, 90% of a song's units came from Class Light Blue and Class Pink (midpoint = 45%); of this, 55% were from Class Light Blue and 35% were from Class Light Pink). In these 14 cases, the ratio of the two backbone Classes would be closer to equal than not, as if the KO mouse were attempting to balance the semantic groupings. Of the remaining, less equalized mice, all save one mouse had a majority of their backbone vocalizations from Class Light Pink, almost as if these mice had determined that the backbone should be made out of one correct class as opposed to the other.

The KO mice in this manipulation showed the beginning of banding patterns similar to the syntax in the WT mice [describe on figure). However, the Classes are not consistent. If the KO mice had mastered the semantics involved in global contextual usage of Classes, one would expect equivalent clustering – in other words, all the calls in Class Green in the WT corpus would be in the same Class in the KO corpus (regardless of what it was called), not in three different "Classes. The KO mice have enough of a grasp on the song to use syntax to some extent, but do not have enough of a grasp of semantics to use more complex patterns of global co-occurrence.

From the perspective of high-dimensional modeling, it is interesting to think of this differentiation between syntax and semantics in a way similar to the high dimensional vectors built in Latent Semantic Analysis (LSA; Landauer & Dumais, 1997). The computational vectors in LSA are built from semantic word representations, which are abstract and gleaned over multiple experiences, and episodic contextual representations (Landauer & Dumais, 1997). Another perspective on these results might be that the KO mice are lacking in the abstract semantic portions (or equivalents thereof) to their call vectors, thus leaving them quite literally in the middle of a contextual representation – that of song in the context of courtship – but not the correct abstract knowledge to put together a meaningful sequence of vocalizations.

The ideas explored in the results of both of these manipulations are an important parallel to a classic symptom of fragile X in humans. Clinical signs of fragile X include problems with rate or speed of speech, including stuttering or repetition (Abbeduto & Hagerman, 1998). This may be represented in the case of the KO mice as problematic syntax. Furthermore, it is important to note that the syntax deficiency is specifically due to repetitions, which, in terms of the KO mice – very plausibly might be expressed as repetitions of individual calls (as opposed to members of a Class). In addition, with humans, there are impairments to lexical development in fragile X syndrome, which may be manifested in an ability to master a vocabulary (calls), but not a semantic grammar (Classes) (Abbeduto & Hagerman, 1998).

REFERENCES:

- Abbeduto, L., Brady, N., & Kover, S. T. (2007). Language development and fragile X syndrome: Profiles, syndrome-specificity, and within-syndrome differences. *Mental Retardation and Developmental Disabilities Research Reviews, 13*(1), 36-46.
- Abbeduto, L., & Hagerman, R. J. (1997). Language and communication in fragile X syndrome. *Mental Retardation and Developmental Disabilities Research Reviews, 3*(4), 313-322.
- Abbeduto, L., & Hagerman, R. J. (1998). Language and communication in fragile X syndrome. *Mental Retardation and Developmental Disabilities Research Reviews, 3*(4), 313-322.
- Baker, M. C., & Gammon, D. E. (2008). Vocal memes in natural populations of chickadees: why do some memes persist and others go extinct. *Animal Behaviour, 75*(1), 279-289.
- Bartholemy, M., Gourbal, B. E. F., Gabrion, C., & Petit, G. (2004). Influence of the female sexual cycle on BALB/c mouse calling behaviour during mating. *Naturwissenschaften, 91*(135-138).
- Beecher, M. D., Burt, J. M., O'Loghlen, A. L., Templeton, C. N., & Campbell, S. E. (2007). Bird song learning in an eavesdropping context. *Animal Behaviour, 73*(6), 929-935.
- Belzner, S., Voigt, C., Catchpole, C. K., & Leitner, S. (2009). Song learning in domesticated canaries in a restricted acoustic environment. *Proceedings of the Royal Society B: Biological Sciences, 276*(1669), 2881-2886. doi: 10.1098/rspb.2009.0669
- Bohn, K. M., Schmidt-French, B., Ma, S. T., & Pollak, G. D. (2008). Syllable acoustics, temporal patterns, and call composition vary with behavioral context in Mexican free-tailed bats. *The Journal of the Acoustical Society of America, 124*(3), 1838-1848.
- de la Torre, S., & Snowden, C. T. (2009). Dialects in pygmy marmosets? Population variation in call structure. *American Journal of Primatology, 71*(4), 333-342.
- Deecke, V. B., Ford, J. K. B., & Spong, P. (2000). Dialect change in resident killer whales: implications for vocal learning and cultural transmission. *Animal Behaviour, 60*, 629-638.
- Deecke, V. B., & Janik, V. M. (2006). Automated categorization of bioacoustic signals: Avoiding perceptual pitfalls. *Journal of the Acoustical Society of America, 119*(1), 645-653.
- Fehér, O., Wang, H., Saar, S., Mitra, P. P., & Tchernichovski, O. (2009). De novo establishment of wildtype song culture in the zebra finch. *Nature, 459*(7246), 564-568.
- Feng, A. S., Narins, P. M., Xu, C.-H., Lin, W.-Y., Yu, Z.-L., Qiu, Q., et al. (2006). Ultrasonic communication in frogs. *Nature, 440*, 333-336.
- Fujita, E., Tanabe, Y., Shiota, A., Ueda, M., Suwa, K., Momoi, M. Y., et al. (2008). Ultrasonic vocalization impairment of Foxp2 (R552H) knockin mice related to speech-language disorder and abnormality of Purkinje cells. *Proceedings of the National Academy of Sciences, 105*(8), 3117-3122.
- Guo, Z., & Holy, T. E. (2007). Sex selectivity of mouse ultrasonic songs. *Chem Senses, 32*(5), 463-473.
- Hammerschmidt, K., Radyushkin, K., Ehrenreich, H., & Fischer, J. (2009). Female mice respond to male ultrasonic songs with approach behaviour. *Biology Letters, 5*(5), 589-592. doi: 10.1098/rsbl.2009.0317
- Holtzman, D. M., Santucci, D., Kilbridge, J., Chua-Couzens, J., Fontana, D. J., Daniels, S. E., et al. (1996). Developmental abnormalities and age-related neurodegeneration in a mouse model of Down syndrome. *Proceedings of the National Academy of Sciences, 93*, 13333-13338.
- Holy, T. E., & Guo, Z. (2005). Ultrasonic songs of male mice. *Plos Biology, 3*(12), 1-10.
- Janik, V. M. (1999). Pitfalls in the categorization of behaviour: A comparison of dolphin whistle classification methods. *Animal Behavior, 57*, 133-143.
- Jarvis, E. D., Scharff, C., Grossman, M. R., Ramos, J. A., & Nottebohm, F. (1998). For whom the bird sings: context-dependent gene expression. *Neuron, 21*(4), 775-788.
- Kapusta, J., & Sales, G. D. (2009). Male-female interactions and ultrasonic vocalization in three sympatric species of voles during conspecific and heterospecific encounters. *Behaviour, 146*, 939-962.
- Kover, S. T., & Abbeduto, L. (2010). Expressive language in male adolescents with fragile X syndrome with and without comorbid autism. *Journal of Intellectual Disability Research, 54*, 246-265.
- Lai, C. S. L., Fisher, S. E., Hurst, J. A., Vargha-Khadem, F., & Monaco, A. P. (2001). A forkhead-domain gene is mutated in a severe speech and language disorder. *Nature, 413*(6855), 519-523.
- Lammers, M. O., Au, W. W. L., & Herzing, D. L. (2003). The broadband social acoustic signaling behavior of spinner and spotted dolphins. *The Journal of the Acoustical Society of America, 114*(3), 1629- 1639.
- Landauer, T. K., & Dumais, S. T. (1997). A solution to Plato's problem: The latent semantic analysis theory of acquisition, induction, and representation of knowledge. *Psychological Review, 104*(2), 211- 240.
- Madsen, P. T., & Wahlberg, M. (2007). Recording and quantification of ultrasonic echolocation clicks from free-ranging toothed whales. *Deep Sea Research Part I: Oceanographic research papers, 54*(8), 1421-1444.
- Musolf, K., Hoffmann, F., & Penn, D. J. (2010). Ultrasonic courtship vocalizations in wild house mice, Mus musculus musculus. *Animal Behaviour, 79*(3), 757-764.
- Nakano, R., Takanashi, T., Fujii, T., Skals, N., Surlykke, A., & Ishikawa, Y. (2009). Moths are not silent, but whisper ultrasonic courtship songs. *J Exp Biol, 212*(24), 4072-4078. doi: 10.1242/jeb.032466
- Nelson, D. A., & Poesel, A. (2009). Does learning produce song conformity or novelty in white-crowned sparrows, Zonotrichia leucophrys? *Animal Behaviour, 78*(2), 433-440.
- Nyby, J. (1983). Ultrasonic vocalizations during sex behavior of male house mice (Mus musculus): a description. *Behavioral and neural biology, 39*(1), 128-134.
- Pepperberg, I. M. (1994). Vocal learning in grey parrots (Psittacus erithacus): Effect of social interaction, reference, and context. *Auk, 111*(2), 300-313.
- Picker, J. D., Yang, R., Ricceri, L., & Berger-Sweeney, J. (2006). An altered neonatal behavioral phenotype in Mecp2 mutant mice. *Neuroreport, 17*(541-544).
- Pomerantz, S. M., Nunez, A. A., & Bean, N. J. (1983). Female behavior is affected by male ultrasonic vocalizations in house mice. *Physiological Behavior, 31*, 91-96.
- Price, J. R., Roberts, J. E., Hennon, E. A., Berni, M. C., Anderson, K. L., & Sideris, J. (2008). Syntactic complexity during conversation of boys with fragile X syndrome and Down syndrome. *Journal of Speech Language and Hearing Research, 51*(1), 3-15.
- Putland, D. A., Nicholls, J. A., Noad, M. J., & Goldizen, A. W. (2006). Imitating the neighbours: vocal dialect matching in a mimic–model system. *Biology Letters, 2*(3), 367.
- Rendell, L. E., & Whitehead, H. (2001). Culture in whales and dolphins. *Behavioral and Brain Sciences, 24*(2), 309-+.
- Roberts, J. E., Hennon, E. A., Price, J. R., Dear, E., Anderson, K., & Vandergrift, N. A. (2007). Expressive language during conversational speech in boys with fragile X syndrome. *American Journal on Mental Retardation, 112*(1), 1-17.
- Roberts, J. E., Price, J., Barnes, E., Nelson, L., Burchinal, M., Hennon, E. A., et al. (2007). Receptive vocabulary, expressive vocabulary, and speech production of boys with fragile X syndrome in comparison to boys with Down syndrome. *American Journal on Mental Retardation, 112*(3), 177- 193.
- Scattoni, M. L., Crawley, J., & Ricceri, L. (2009). Ultrasonic vocalizations: A tool for behavioural phenotyping of mouse models of neurodevelopmental disorders. *Neuroscience & Biobehavioral Reviews, 33*(4), 508-515.
- Scearce-Levie, K., Roberson, E. D., Gerstein, H., Cholfin, J. A., Mandiyan, V. S., Shah, N. M., et al. (2007). Abnormal social behaviors in mice lacking Fgf17. *Genes Brain and Behavior, 7*(5), 344- 354.
- Sudhalter, V., Maranion, M., & Brooks, P. (1992). Expressive Semantic Deficit in the Productive Language of Males With Fragile X Syndrome. *American Journal of Medical Genetics, 43*, 65-71.
- Sutcliffe, J. S., Nelson, D. L., Zhang, F., Pieretti, M., Caskey, C. T., Saxe, D., et al. (1992). DNA methylation represses FMR-1 transcription in fragile X syndrome. *Human Molecular Genetics, 1*, 397-400.
- The Dutch-Belgian Fragile X Consortium. (Bakker CE, V. C., Willemsen R, van der Helm R, Oerlemans F, Vermey M, Bygrave A, Hoogeveen AT, Oostra BA, Reyniers E, et al.). (1994). Fmr1 knockout mice: a model to study fragile X mental retardation. *Cell, 78*, 23-33.
- Toro, J. M., & Trobalon, J. B. (2005). Statistical computations over a speech stream in a rodent. *Perception & Psychophysics, 67*(5), 867-875.
- Tyack, P. L. (2008). Convergence of calls as animals form social bonds, active compensation for noisy communication channels, and the evolution of vocal learning in mammals. *Journal of Comparative Psychology, 122*(3), 319-331.
- Wheelwright, N. T., Swett, M. B., Levin, I. I., Kroodsma, D. E., Freeman-Gallant, C. R., & Williams, H. (2008). The influence of different tutor types on song learning in a natural bird population. *Animal Behaviour, 75*(4), 1479-1493.
- White, N. R., Prasad, M., Barfield, R. J., & Nyby, J. G. (1998). 40- and 70-kHz vocalizations of mice (Mus musculus) during copulation. *Physiological Behavior, 63*, 467-473.
- Wohr, M., & Schwarting, R. K. (2007). Ultrasonic communication in rats: can playback of 50-kHz calls induce approach behavior? *PLoS One, 2*(12), e1365.
- Wright, T. F., Dahlin, C. R., & Salinas-Melgoza, A. (2008). Stability and change in vocal dialects of the yellow-naped amazon. *Animal Behaviour, 76*(3), 1017-1027.
- Zann, R. A. (1996). *The Zebra Finch: A Synthesis of Field and Laboratory Studies*. New York: Oxford University Press.

CHAPTER 5: CONCLUSION

Cosmo

This study, despite the limitation of being conducted on a single subject, provides considerable insight into the cognitive abilities of an African Gray Parrot. A power study such as this provides information on the capabilities of a species by measuring the abilities of one individual. If an individual in a species is able to demonstrate a particular cognitive capacity with reliability, it can be assumed that the entire species possesses the mechanical *capabilities* for such cognition, regardless of the extent to which these abilities are displayed (Lloyd, 2004; Triana & Pasnak, 1981).

It appears that Cosmo can exploit the patterns of statistical regularity in language, and, in particular, global co-occurrence, in her language learning. The HAL model, which detects these language patterns, was able to identify meaningful clusters within Cosmo's speech. When Cosmo's speech was input into the model as individual words, the co-occurrence clusters that appeared were similar to those found in humans (albeit less definitive); words that Cosmo used in similar contexts were grouped together. This pattern also held at a phrase level; when Cosmo's utterances were entered into the HAL model in phrase form, the clusters which resulted had contextual themes – for example, contact calls or vocalizations dealing with the telephone. These phrases show the same global co-occurrence patterns within conversations (or their equivalent) as words do within sentences.

In addition, coincident with working with the HAL model, several other insights into Cosmo's language abilities became apparent. Cosmo has several distinct areas in which she shows an ability to create novelties in language, namely unique phrase constructions, humor, and the generalization and transfer of word meaning. Cosmo consistently uses phrases that are agrammatical in human language; however they cluster normally within their intended contextual groups as one would expect with a model like HAL. These are phrases Cosmo has created. BJ would not use grammar this awkward, and thus Cosmo could not have copied the phrases (as such) from her. Yet, Cosmo still uses them in the correct context; she is not randomly playing with or re-arranging words. The HAL model, when analyzing typed

human language, will group "the" and the typo "teh", because they occur in the same context (Burgess, 1998; Burgess & Lund, 2000; Lund & Burgess, 1996). This type of grouping is a nearly identical circumstance to Cosmo's agrammatical usage, the only difference is that Cosmo has "created" the "typo" (and consistently uses it).

Cosmo also demonstrates humor of her own creation. After learning that birds have feathers, dogs have fur, and people wear clothes, she mixes and matches with "jokes" such as "Mary (the dog) has feathers!" and then loudly scolds herself "Nooooo! Mary has fur!" In addition to the humor in these phrases, they are also uniquely Cosmo's creation.

Lastly, Cosmo provides evidence of the ability to generalize meaning. She uses words referentially and has multiple labels for one object. She is also able to substitute words in context, having learned "you have reached … [phone number]" as an answering machine message, and subsequently creating her own phrases by plausibly substituting a variety of words (for example, "Betty Jean") for the phone number.

Because this study used $N = 1$, it is an understatement to say that more research is necessary before any definitive generalizations with regards to anything beyond the basic capability can be drawn. However, the language abilities demonstrated here by an African gray parrot support the idea that the species may indeed possess the substrate necessary for many higher cognitive functions (Kako, 1999).

Humpback Whales

One of the initial goals of this research was to provide support for the existence of cultural clans in humpback whales by showing dialects that were unique to regions, but seemed to share traits with nearby regions or across periods of time. There is some evidence for this in the case of songs recorded in Puerto Rico, which is located geographically between the Lesser Antilles and Turks and Caicos (the other two locations in which data were recorded). The songs in Puerto Rico were much more diverse than the songs recorded in the other locations. It was also harder, in this region, to identify a uniform, overall, region-

103

specific pattern in the songs. However, the songs did share some characteristics of the songs recorded in the other two areas; most notably, there was a similarity between song70 and song74 (Puerto Rican songs), and song171 (recorded in the Lesser Antilles).

Songs recorded in both the Lesser Antilles and in Turks and Caicos show signs of change by forms of dispersion, or spreading, of song patterns (or lack thereof). The Turks and Caicos songs are uniform and conform to a fairly strict set of rules. In addition, the vocabulary (both number of unit types and number of Class types) used by whales in this area is limited. This small vocabulary may be indicative of a population that is isolated by geography to some extent, and that, as a result, is not exposed to songs from other populations; these factors might also result in additional, region specific novelties. Thus, this limited vocabulary could be indicative of a newly developing population that is just establishing a distinct dialect and, therefore, would show a specific necessity to maintain a clear, easy-to-sing dialect with few elements in order to promote retention. In the Lesser Antilles, there is possible evidence of the divergence of songs over time, as in 1973 the songs measured are far more similar to each other than those measured in 1976. This is roughly the same pattern that would be expected in the future for the songs from the Turks and Caicos (Putland, Nicholls, Noad, & Goldizen, 2006; Rendell & Whitehead, 2005; Weilgart & Whitehead, 1997).

Additionally, the results provide support for global co-occurrence in humpback whale song, as many of these patterns (plus the song backbones) would not have been identifiable without initially identifying the Class that is encoded in the statistical regularities of the song sequences. Classes, whether they are semantic or grammatical or represent a combination of the two language components, do appear to be involved in the creation of humpback whale song. These patterns, which may be similar to patterns in human language, could be identified in all of the songs. For example, one could compare the English grammar pattern noun + verb + direct object to a pattern in the humpback song such as Class Light Blue + Class Dark Blue + Class Light Purple. In both cases, the categories (be they human grammar or whale Class) consist of a variety of individual elements, and any of these elements would serve the proper contextual purpose in the pattern or sentence.

104

Mice

The goal of the manipulations presented here was a comparison of male courtship songs from a group of *Fmr1* knockout mice – which are used as a model for fragile X syndrome – to normal, or "wild type" mice.

HAL analysis reveals that the KO mice appear to have limited use of syntax, but that their syntactic patterns are formed at the local co-occurrence level only. For example, the songs of WT mice are characterized by a backbone made from one particular Class. HAL analysis shows the calls in this Class to be contextually similar, and tokens in the backbone can come from any of the four calls in the Class. The same four calls appear with very high frequency in the songs of the KO mice, and if they are coded with the Classes established by the WT mice, it is apparent that they could form a backbone. However, the matrix built from the KO corpus shows that these mice do not use the same global co-occurrence clusters as the WT mice (which, for purposes of this experiment, were assumed to be an appropriate baseline). HAL does not identify the four calls that create the backbone in the WT corpus as a Class in the KO corpus. Therefore, the KO mice are only able to create songs with the correct syntax because they are putting together the backbone of the song at a local level. To phrase it differently, KO mice create the background of their songs by creating sequences of call1, call4, call5, and call9, while WT mice build their songs by creating sequences of calls from Class Yellow (the class which contains these calls).

When examining the Classes created from global co-occurrence directly in the KO corpus, the ways in which the KO mice are creating their songs and the "mistakes" they are making (in comparison to the WT mice) become more apparent. Using the KO corpus and mapping on the "correct" Classes obtained in the WT analysis, a rough comparison can be made between the co-occurrence structure in the KO mice and what it might have been had they been using the typical contextual relationships (relative to what they are using in reality). KO mice divide the four calls in the backbone (Class Yellow) into two Classes in their own dialect (for lack of a better word). However, there appears to be a tendency toward a higher frequency of one Class over the other, creating the possibility that the KO mice have some sense of what "should be"

happening. In addition, the KO mice show patterns of drop-in calls that are very similar to those of the WT mice; however, these patterns exist because of call identification – not Class. For example, if we coded a drop in of call17 using the "correct" Classes, it would appear as a Class Green token in a Class Yellow backbone. However, using KO Classes, it appears as a Class Beige token in a Class Pink backbone. This would be appropriate, if the other members of WT Class Green were *also* members of KO Class Beige – but they are not. Again, the WT mice are using a system in which they can pick any call from a particular Class, whereas the KO mice are confined to building syntactic patterns with specific call type.

Currently, conclusions from the literature dealing with the language impairments in fragile X syndrome in humans lack consistency. There is evidence that links the language deficit to problems with expressive semantics, or difficulty retrieving the word desired from already learned vocabulary to complete the expression of a thought (Sudhalter, Maranion, & Brooks, 1992). The results here support this mechanism for language difficulties. Other studies, however, have shown that there is a delay in the learning of syntax in people with fragile X syndrome (Roberts, Hennon, Price, Dear, Anderson, & Vandergrift, 2007; Price, Roberts, Hennon, Berni, Anderson, & Sideris, 2008). The study here provides evidences contrary to this, as the KO mice showed signs of being able to appropriately use syntax, at least on a local level.

High dimensional modeling of language acquisition in humans and animals

High dimensional modeling in linguistics has never erred on the side of traditionalism. Starting in the 1990's, high dimensional models such as the SRN, HAL, and LSA challenged the traditional notions of innate natural language and began to replace traditional theories of language acquisition ("Induction explained?", 1997). The expansion of this success into the arena of animal communication is unsurprising proof of their universal applicability. In fact, a recent paper has even used emergent models to account for aspects of the more traditional language acquisition models they themselves replaced. Mayor and Plunkett (2010) recently assembled a computational model based on self organizing maps that accounts for, among other things, fast mapping as a method of language acquisition and the rapidity with which language is

106

learned in early childhood – both ideas (or part of ideas, as is the case of rapid language learning in the minimalist program) which likely should - and will - be replaced with emergent language theories.

High dimensional models such as HAL and LSA have introduced a new perspective on language acquisition in humans, that language is an emergent property that can be learned via a simple inductive mechanism despite a seemingly "impoverished stimulus." The evidence of global co-occurrence patterns in animal vocalization presented here further supports this idea as it adds to a general convergence of evidence. This is particularly true because of the novelty of the situation – animal vocalizations – the continued robustness of the high dimensional approach in such a situation extends the universality of the models application.

Limitations of these studies

As mentioned in earlier chapters, much of the work presented here is novel. Because higher cognitive issues in non-human species are addressed, these results will naturally – and rightfully – be regarded with skepticism. However, this is only the second time that a concept such as contextual cooccurrence has been applied to animal vocalizations of any sort (McCowan, Doyle, Kaufman, Hanser & Burgess, 2008), and the results have been sufficiently encouraging to warrant further exploration.

The humpback whale and mouse studies are also limited by the fact that there is no way to understand the meanings of the classes that cluster as a result of the statistical regularities in the input stream. In the Cosmo study, it is easy to discern the success or failure of an analysis, because the results "make sense" in that one can understand them by human experience. The only recourse available in the other studies is playback, which is logistically complicated and technologically sophisticated. In light of this limitation, every effort has been made to make appropriate choices regarding model parameters. For example, efforts were made to gather opinions from those who work with the study specimens and to apply what is known from communication systems, such as the idea that the most stable structure is the preferred one.

Lastly, statistical techniques for the confirmation of many the patterns identified in this study have not been worked out. The color coding technique was developed specifically for these experiments as a method of visualizing patterns of Classes, as opposed to individual units. Techniques such as the entropy analysis help identify common patterns in the data; however, due to their categorical nature, there is little beyond qualitative description that can be used to describe the patterns once they have been found.

Future studies

 Before anything can be definitively stated about the use of global co-occurrence in animal communication, other successful studies must be conducted and the parameters used in models need to be successfully standardized. In addition, a universal technique for examining data such as these must be adopted – be it the color-coded analysis developed and presented here, or some other technique.

One important way to validate the idea that global co-occurrence is a relevant construct in animal communication systems is by subjecting vocalization streams such as the ones tested here to other models similar to the HAL model - which operate by very different mechanisms, yet produce similar results. Two models that are closely related to HAL are Latent Semantic Analysis (LSA; Landauer, Foltz, & Laham, 1998) and the Simple Recurrent Network (SRN; Elman, 1990). Both models - like HAL - learn from context and without outside training, and both models have shown similar results with similar data sets (Burgess & Lund, 2000; Yan, Li, & Song, 2004). These models would be the most appropriate starting point for a comparative model of these types of models but also the theory they test..

It may also be worthwhile to examine new corpuses for analysis. Two traits, absent in these three experiments, would be particularly appealing: a smaller-sized and/or more discernable vocabulary, and the availability of behavioral data. The former, as a problem, is strikingly evident in the lack of progress that has been made on dolphin vocalizations; this species is by far the most well studied of all the marine mammals, the most accessible (in both captivity and in the wild), and the species for which behavioral data are easiest to obtain. However, because the dolphin whistle stream is extraordinarily hard to segment and classify into individual tokens, very little progress has been made beyond the issues under debate, and into

concepts such as syntax and structure (Buck & Tyack, 1993; Deecke, 2006; Deecke & Janik, 2006; Janik, 1999; McCowan & Reiss, 1997, 2001; Sayigh, Esch, Wells, & Janik, 2007). With the exception of the large literature on signature whistles, which are theorized to be "names" (Caldwell & Caldwell, 1965), there is only a single study that has examined meaning in dolphin whistles (McCowan, Doyle, Kaufman, Hanser, & Burgess, 2008). A communication repertoire in which individual elements are much more readily defined – for example, the time dependant codas of sperm whales or a particularly well categorized species of bird's song-- would be particularly desirable for the type of analyses discussed here. In addition, while a small corpus limits generalizability and precision, corpuses with as many synonyms or as large of a vocabulary as the corpus used for the Cosmo experiments can also be unwieldy.

In the absence of "word" meaning knowledge, behavioral data would be a major asset. The ability to understand the words spoken by a parrot is an undeniable bonus to the amount and nature of conclusions that can be drawn. The availability of behavioral data that is paired with the communication stream would provide some context in which to place the communication and offer the possibility of making inferences about the meaning of the classes of information.

The advantage of being able to understand the Cosmo corpus (or that of any other languagespeaking parrot) also enables the use of additional linguistic models. Programs such as Linguistic Inquiry and Word Count (LIWC; Pennebaker, Francis, & Booth, 2001) are particularly aimed at analyzing usage of concepts such as emotion words, positive and negative connotations, first and third person references, and other details of language that we might describe as "human like." A comparison of these concepts could prove insightful into the cognition of the species being studied.

"backbone structure" found in both the humpback whale and mouse corpuses, is an important finding in this research. Initially, this backbone and the proposed "drop in" units may appear counter-intuitive to the patterning that was discussed as evidence of global co-occurrence. However, this is not the case. Returning to the example of the Elman corpus in Figure 10, we can also create Figure 21 by broadening the noun class to include direct objects. Upon doing this, a purple backbone becomes evident.

The introduction of the

Further studies on the parameters that create the backbone class could be theoretically important from a syntactic perspective.

Lastly, the use of less traditional measures such encephalization quotient or innovative ability may prove fruitful in providing direction for the selection of promising species for study. Many of the communication systems of species that are "traditionally" thought of as intelligent are already being studied; these include species such as great apes, marine mammals, monkeys, parrots, corvids, elephants, and carnivores such as pinnipeds and, more recently, dogs. However, other markers for intelligence might open up other promising species as subjects for investigation; marmots and foxes for their relatively higher EQ's, Australian bowerbirds for their innovative abilities, pigs for their rapid learning, octopuses for their

problem solving abilities, otters for their elaborate play, and several species of birds for their tool use and innovative techniques for prey capture (Broom, Sena, & Moynihan, 2009; Finn, Tregenza, & Norman, 2009; Keagy, Savard, & Borgia, 2009; Lefebvre, 1995; Lefebvre, Nicolakakis, & Boire, 2002; Ralls & Siniff, 1990; Roth, 2003; Werdenich & Huber, 2006).

Benefits of this research

The benefits of the research presented here encompass both theoretical and practical arenas. From a theoretical perspective, the idea of the evolution of language is a hotly debated topic in recent academic literature (Hauser, Chomsky, & Fitch, 2002). The comparative perspective taken here is a vital one; it is only from a truly cross-species, comparative, perspective that we can really hope to understand the selective pressures that have shaped the evolution of language. By finding common (or lack of common) threads in communication capabilities among species, we can trace what environmental conditions may have been conducive for the analogous development of such abilities in species as diverse as birds and land and sea mammals.

The most important, general theoretical result from this research has been the discovery that some animals have statistical regularities in their communication that carry sophisticated information reflective of a range of categorical knowledge. Simple regularities, such as conditional probabilities, have been identified by others; however, these results represent a much higher-order level of knowledge.

From a practical perspective, any insight into the evolution of language will bring us one step closer to understanding the variety of language deficits and deficiencies that plague so many people. The *Fmr1* knockout mice discussed here provide a perfect example of this insight; while symptoms of fragile X syndrome can be created in mice for the purposes of experimental treatment and pharmacology, the root cause of the symptoms (such as deficits in linguistic abilities) can only be understood by identifying them specifically and comparing them to "normal" models. This comparison and the resulting information will be vital to treatment.

Understanding the complexities of communication and category learning in animals and what the categories might represent will be a key step in the future development of animal communication. In both the effort to understand the evolution of our own communicative abilities, and in the challenges faced in overcoming language impairments, the thoughts of the Chinese General Sun Tzu are particularly appropriate: "Know your enemy and know yourself and you can fight a hundred battles without disaster."

REFERENCES:

- Broom, D. M., Sena, H., & Moynihan, K. L. (2009). Pigs learn what a mirror image represents and use it to obtain information. *Animal Behaviour, 78*(5), 1037-1041.
- Buck, J. R., & Tyack, P. L. (1993). A quantitative measure of similarity for tursiops truncatus signature whistles. *The Journal of the Acoustical Society of America, 94*(5), 2497-2506.
- Burgess, C., & Lund, K. (2000). The Dynamics of Meaning in Memory. In E. Dietrich & A. B. Markman (Eds.), *Conceptual and Representational Change in Humans and Machines* (pp. 117-156). Mahwah, New Jersey: Lawrence Erlbaum Associates.
- Caldwell, M. C., & Caldwell, D. K. (1965). Individualized Whistle Contours in Bottle-nosed Dolphins (Tursiops truncatus). *Nature, 207*, 434-435.
- Deecke, V. B. (2006). Studying Marine Mammal Cognition in the Wild: A Review of Four Decades of Playback Experiments. *Aquatic Mammals, 32*, 461-482.
- Deecke, V. B., & Janik, V. M. (2006). Automated categorization of bioacoustic signals: Avoiding perceptual pitfalls. *Journal of the Acoustical Society of America, 119*(1), 645-653.
- Elman, J. L. (1990). Finding structure in time. *Cognitive Science, 14*, 179-211.
- Finn, J. K., Tregenza, T., & Norman, M. D. (2009). Defensive tool use in a coconut carrying octopus. *Current Biology, 19*(23), R1069-R1070.
- Hauser, M. D., Chomsky, N., & Fitch, W. T. (2002). The faculty of language: What is it, who has it, and how did it evolve? *Science, 298*(5598), 1569-1579.
- Induction explained? (1997). *Trends in Cognitive Sciences, 1*(5), 159.
- Janik, V. M. (1999). Pitfalls in the categorization of behaviour: A comparison of dolphin whistle classification methods. *Animal Behavior, 57*, 133-143.
- Kako, E. (1999). Elements of syntax in the systems of three language-trained animals. *Animal Learning Behavior, 27*(1), 1-14.
- Keagy, J., Savard, J.-F., & Borgia, G. (2009). Male satin bowerbird problem-solving ability predicts mating success. *Animal Behaviour, 78*(4), 809-817.
- Landauer, T. K., Foltz, P. W., & Laham, D. (1998). Introduction to Latent Semantic Analysis. *Discourse Processes, 25*, 259-284.
- Lefebvre, L. (1995). The opening of milk bottles by birds: Evidence for accelerating learning rates, but against the wave-of-advance model of cultural transmission. *Behavioral Processes, 34*, 43-54.
- Lefebvre, L., Nicolakakis, N., & Boire, D. (2002). Tools and brains and birds. *Behaviour, 139*, 939-973.
- Lloyd, E. (2004). Kanzi, evolution, and language. *Biology & Philosophy, 19*(4), 577-588.
- Mayor, J., & Plunkett, K. (2010). A neurocomputational account of taxonomic responding and fast mapping in early word learning. *Psychological Review, 117*(1), 1-31.
- McCowan, B., Doyle, L. R., Kaufman, A. B., Hanser, S. F., & Burgess, C. (2008). Detection and estimation of complexity and contextual flexibility in nonhuman animal communication systems. In U. Griebel & K. Oller (Eds.), *Evolution of Communicative Flexibility: Complexity, Creativity, and Adaptability in Human and Animal Communication (pp. 281-304). Cambridge, MA: MIT Press.* Cambridge: MIT Press.
- McCowan, B., & Reiss, D. (1997). Quantitative comparison of whistle repertoires from captive adult bottle-nosed dolphins (Delphinidae, Tursiops-Truncatus) - a reevaluation of the signature whistle hypothesis. *Ethology, 100*(3), 194-209.
- McCowan, B., & Reiss, D. (2001). The fallacy of `signature whistles' in bottlenose dolphins: a comparative perspective of `signature information' in animal vocalizations. *Animal Behavior, 62*(6), 1151- 1162.
- Pennebaker, J. W., Francis, M. E., & Booth, R. J. (2001). *Linguistic Inquiry and Word Count (LIWC): LIWC2001*. Mahwah: Lawrence Erlbaum Associates.
- Putland, D. A., Nicholls, J. A., Noad, M. J., & Goldizen, A. W. (2006). Imitating the neighbours: vocal dialect matching in a mimic–model system. *Biology Letters, 2*(3), 367.
- Price, J. R., Roberts, J. E., Hennon, E. A., Berni, M. C., Anderson, K. L., & Sideris, J. (2008). Syntactic complexity during conversation of boys with fragile X syndrome and Down syndrome. Journal of Speech Language and Hearing Research, 51(1), 3-15
- Ralls, K., & Siniff, D. B. (1990). Time Budgets and Activity Patterns in California Sea Otters. *The Journal of Wildlife Management, 54*(2), 251-259.
- Roth, G. (2003). Is the human brain unique? In M. Brüne, H. Ribbert & W. Schiefenhövel (Eds.), *The social brain: Evolution and pathology*. Hoboken: Wiley.
- Rendell, L. E., & Whitehead, H. (2005). Spatial and temporal variation in sperm whale coda vocalizations: stable usage and local dialects. *Animal Behavior, 70*(1), 191-198.
- Roberts, J. E., Hennon, E. A., Price, J. R., Dear, E., Anderson, K., & Vandergrift, N. A. (2007). Expressive language during conversational speech in boys with fragile X syndrome. American Journal on Mental Retardation, 112(1), 1-17.
- Sayigh, L. S., Esch, H. C., Wells, R. S., & Janik, V. M. (2007). Facts about signature whistles of bottlenose dolphins, Tursiops truncatus. Animal Behaviour, 74(6), 1631-1642.
- Sudhalter, V., Maranion, M., & Brooks, P. (1992). Expressive Semantic Deficit in the Productive Language of Males With Fragile X Syndrome. *American Journal of Medical Genetics, 43*, 65-71.
- Triana, E., & Pasnak, R. (1981). Object permanence in cats and dogs. *Animal Learning & Behavior, 9*, 135- 139.
- Weilgart, L., & Whitehead, H. (1997). Group-specific dialects and geographical variation in coda repertoire in South Pacifc sperm whales. *Behav Ecol Sociobiol, 40*, 277-285.
- Werdenich, D., & Huber, L. (2006). A case of quick problem solving in birds: string pulling in keas, Nestor notabilis. *Animal Behaviour, 71*(4), 855-863.
- Yan, X., Li, X., & Song, D. (2004). A Correlation Analysis on LSA and HAL Semantic Space Models. In Y. Fu, J. Han & J. Zhang (Eds.), *Computational and Information Science, First International Symposium, CIS 2004* (pp. 711-717). Shanghai, China.

APPENDIX A

Complete repertoire for Cosmo, plus abbreviations of sounds. An "s" on the end of a sound denotes a

sequence.

APPENDIX B

Humpback whale vocalizations, by song. PR = Puerto Rico, TC = Turks and Caicos, LA = Lesser Antilles.

APPENDIX C

Wild Type mice corpuses, coded with classes. Numbers are identifiers for individual mice.

				c1		
				c1		
				c1		
				c1		
				c7		
				c1		
				c13		
				c1		
				c12		
				c1		
				c1		
				c4		
				c12		
				c1		
				c10		
				$\mathtt{c}12$		
				c6		
				c1		
				c ₉		
				c12		
				c12		
				c10		

Knockout mice corpuses, coded with classes. Numbers are identifiers for individual mice. Ten

particularly short songs $(40 calls) have been removed due to space restrictions.$

APPENDIX D

Frequency counts for all corpuses

COSMO:

HUMPBACK SONG:

By song. PR = Puerto Rico, TC = Turks and Caicos, LA = Lesser Antilles.

					ТC	TС	TС	LA	LA	LA	LA
	PR '70	PR '70	PR '70	PR '75	'74	'74	'74	'73	'73	'76	'76
	117770	117774	117775	128296	118102	118118	118119	110847	110858	118171	118172
unit 1	30	12	56	$\mathbf{0}$	$\sqrt{5}$	$\,8$	2	$\mathbf{0}$	$\overline{0}$	50	51
unit 2	$\overline{0}$	$\mathbf{1}$	$\overline{4}$	$\mathbf{0}$	65	112	34	$\overline{2}$	$\mathbf{1}$	$\mathbf{0}$	$\mathbf{0}$
unit 3	14	36	48	$\overline{4}$	70	41	57	71	82	46	49
unit 4	5	14	73	\overline{c}	$\overline{3}$	16	6	90	104	24	28
unit 5	$\boldsymbol{0}$	$\mathbf{0}$	$\mathbf{0}$	$\boldsymbol{0}$	177	121	77	$\boldsymbol{7}$	15	$\mathbf{0}$	$\mathbf{1}$
unit 6	41	14	45	$\boldsymbol{0}$	45	33	34	$\mathbf{0}$	14	93	124
unit 7	105	32	15	$\mathbf{1}$	32	28	52	12	13	61	117
unit 8	$\boldsymbol{7}$	16	19	$\mathbf{1}$	47	64	31	69	57	43	36
unit 9	5	28	46	22	35	33	27	91	82	63	73
unit 10	8	15	46	\mathfrak{Z}	38	44	34	33	33	87	56
unit											
11	$\overline{4}$	$\mathbf{0}$	86	$\overline{0}$	38	85	89	$\overline{0}$	$\overline{0}$	11	\mathfrak{Z}
unit											
12	13	15	56	$\mathbf{0}$	12	44	40	3	τ	61	46
unit 13	54	23	21	$\boldsymbol{0}$	17	22	45	\overline{c}	6	78	94
unit											
14	6	$\overline{4}$	49	$\boldsymbol{0}$	6	$\overline{4}$	$\overline{4}$	51	62	14	14
unit 15	10	28	30	46	$\mathbf{1}$	1	$\overline{0}$	56	$77\,$	43	43
unit 16	97	168	118	$\mathbf{0}$	$\mathbf{1}$	$\overline{4}$	15	$\overline{2}$	$\overline{2}$	71	35
unit											
17	157	64	82	$\boldsymbol{0}$	θ	1	Ω	15	12	40	55
unit 18	32	27	116	6	$\boldsymbol{\mathfrak{Z}}$	Ω	Ω	13	16	32	24
unit											
19	$8\,$	3	32	147	$\mathbf{0}$	θ	Ω	101	62	13	26
unit 20	7	49	81	30	$\boldsymbol{0}$	$\boldsymbol{0}$	$\mathbf{0}$	41	53	20	14
unit											
21	33	52	57	$\boldsymbol{0}$	$\mathbf{1}$	\mathfrak{Z}	$\overline{4}$	57	58	$\overline{4}$	11
unit 22	63	128	79	$\boldsymbol{0}$	$\boldsymbol{\mathfrak{Z}}$	27	12	$\boldsymbol{0}$	$\mathbf{0}$	18	14
unit											
23	22	28	46	$\mathbf{1}$	$\mathbf{1}$	$\sqrt{2}$	\overline{c}	63	59	32	43
unit 24	\overline{c}	3	35	6	$\mathbf{0}$	θ	$\overline{0}$	87	59	18	14
unit											
25	$\mathbf{0}$	\overline{c}	31	22	$\mathbf{0}$	$\boldsymbol{0}$	$\boldsymbol{0}$	54	80	$25\,$	$26\,$
	723	762	1271	291	600	693	565	920	954	947	997

MICE:

