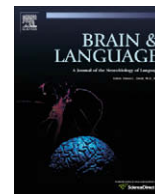




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Vocal learning in Grey parrots: A brief review of perception, production, and cross-species comparisons

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ABSTRACT

This chapter briefly reviews what is known—and what remains to be understood—about Grey parrot vocal learning. I review Greys' physical capacities—issues of auditory perception and production—then discuss how these capacities are used in vocal learning and can be recruited for referential communication with humans. I discuss cross-species comparisons where applicable and conclude with a description of recent research that integrates issues of reference, production and perception.

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1. Introduction

Grey parrot (*Psittacus erithacus*) imitative abilities have been lauded at least since Aristotle. Only fairly recently, however, have we learned how Greys may achieve such feats, how such vocal ability connects to cognitive capacities, and how their abilities compare to other common vocal learners—songbirds, cetaceans, humans, and possibly other mammals. This chapter briefly reviews what is known—and what remains to be understood—about Grey parrot vocal learning. I review Greys' physical capacities—issues of auditory perception and production—then discuss how these capacities are used in vocal learning and can be recruited for referential communication with humans. I discuss cross-species comparisons where applicable and conclude with a description of recent research that integrates issues of reference, production and perception.

2. Physical capacities

2.1. Perception

No studies directly test Grey parrot vocal perception; we infer that Greys perceive sounds at least as well, and in similar ranges, as humans in order to reproduce human vocalizations accurately (see below). Perceptual data do exist for oscine songbirds (e.g., Okanoya & Dooling, 1987) and for psittacids distantly related to Greys: budgerigars (*Melopsittacus undulatus*) and a cockatiel (*Nymphicus hollandicus*; Okanoya & Dooling, 1987), and orange-fronted

conures (*Aratinga canicularis*; Wright, Cortopassi, Bradbury, & Dooling, 2003). These studies suggest both possible parallels and differences among parrots, other avian species, and humans.

For most psittacids and oscines that were tested, regions of both greatest vocal energy and best auditory sensitivity were between 2 and 5 kHz, also the optimal range for human auditory sensitivity (Dooling, 1980; Wright et al., 2003). Such data imply that basic hearing capabilities and the responsible auditory structures are evolutionarily conserved across many species (Dooling, Lohr, & Dent, 2000); however, sensitivities of some hummingbirds, also vocal learners, are at higher ranges (see Ferreira, Smulders, Same-shima, Mello, & Jarvis, 2006; Ficken, Rusch, Taylor, & Powers, 2000). Interestingly, the conure and budgerigar, but neither the cockatiel nor most other avian species so tested (see review, Wright et al., 2003), exhibit critical ratios (signal-to-noise ratio at masked threshold) that differ considerably from those of humans; for most vertebrates, the critical ratio increases by 3 dB/octave (Dooling et al., 2000), whereas for the budgerigar, the ratio is lowest in that same 2–4 kHz window. Such findings suggest, given the phylogenetic and habitat distance of conures and budgerigars (de Kloet & de Kloet, 2005), and the closer relationships between budgerigars and cockatiels, that local effects, such as habitat and sympatric species' vocalizations, may have influenced acoustical niche diversification and evolved perceptual capacities (note Ryan & Brenowitz, 1985).

Other research (e.g., Weisman, Njegovan, Williams, Cohen, & Sturdy, 2004) demonstrates that birds in general, including the budgerigar, discriminate more finely than humans in some domains such as absolute pitch perception. Here, pigeons, a species without significant vocal learning (e.g., ten Cate, Slabbekoorn, & Ballintijn, 2002 data for doves), fall somewhere between humans

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and songbirds (Friedrich, Zentall, & Weisman, 2007). Playback of birdsong at slower speeds than normal reveals considerable complexity missed by human ears; conceivably such detail exists for its usefulness to the birds themselves (Kroodsmas, 2005).

Of interest in terms of the relationship of perception to production, including allospecific production—especially with respect to human speech—are studies demonstrating budgerigar perception of human vowel tokens /i/, /a/, /e/ and /u/ (Dooling, 1992; Dooling & Brown, 1990) and their ability to distinguish consonants /ba-/pa/ (bilabial), /da-/ta/ (alveolar), /ga-/ka/ (velar) (Dooling, Okanoya, & Brown, 1989), /ra-/la/ (Dooling, Best, & Brown, 1995), and /ba-/wa/ consistent with the stimulus-length effect shown in humans (Dent, Pierce, Brittan-Powell, & Dooling, 1997). Clearly, birds perceive sound differences that are critical to production distinctions. Scanlon's (1999) interpretation of similarities in budgerigar and human acoustic features is that budgerigars perceive human speech as modified budgerigar sound. He argues that "...shared neural mechanisms which correspond to these shared acoustic patterns could constitute a phylogenetically conservative level of auditory perception which is communication-sound-specific but not species-specific".

Despite phylogenetic and spatial distances of Greys from the above-mentioned psittacids (i.e., possible separation from Australian parrots 76 MYA and from South American parrots ~35 MYA; de Kloet & de Kloet, 2005), Greys likely have, given the need for perception to underlie production, perceptual abilities similar to birds discussed above. These perceptual abilities are, however, likely a general vertebrate trait: Even animals lacking vocal learning (e.g., chinchillas) perceive some auditory distinctions of human speech (e.g., Kuhl & Miller, 1975).

2.2. Production

Few studies have examined natural Grey parrot vocalizations (imitative: Cruickshank, Gautier, & Chappuis, 1993; conspecific: May, 2004); considerably more is known with respect to their learning human speech, particularly for the Grey, Alex (Pepperberg, 1999). Using standard phonetic and statistical techniques, students and I analyzed spectrograms and videotapes of Alex's speech samples and compared his and my vocalizations (I was his principal trainer). Although Alex's anatomy prevented him from exactly reproducing human articulatory acts, he (though maybe not all parrots) used a two-tube system and frequency modulation, and employed his tongue, glottis, and larynx in some of the same ways used by humans to produce vowels and stop consonants (Patterson & Pepperberg, 1994, 1998; Warren, Patterson, & Pepperberg, 1996). Alex's vowels each exhibited formant structures similar to those of humans (see Fig. 1); his stop consonants exhibited voiced/ voiceless, labial, alveolar, and velar groupings (/p-b/, /d-t/, /g-k/). I summarize only our most relevant findings (details in Patterson & Pepperberg, 1994, 1998; Pepperberg, 2002).

2.2.1. F_0 analyses

We measured fundamental frequencies, F_0 (source vibration at the avian syrinx; syringeal constriction at the tracheal base functionally resembles human vocal folds in phonation; Gaunt & Gaunt, 1985; Scanlan, 1988; Suthers & Zollinger, 2004). F_0 analyses show that Alex, like humans and unlike most songbirds (Greenewalt, 1968; Miller, 1977), used only one set of articulators to produce speech (Larsen & Goller, 1999; Patterson & Pepperberg, 1994)—not by using two halves of his syrinx independently to produce formant-like structure from F_0 's via sine wave interference as Lieberman (1984) suggests. His F_0 s approximated those of an adult human (124–276 Hz, Peterson & Barney, 1952). Even mynahs (*Gracula religiosa*), an oscine, do not use sine wave interference to produce human speech, but their mechanism differs from that of

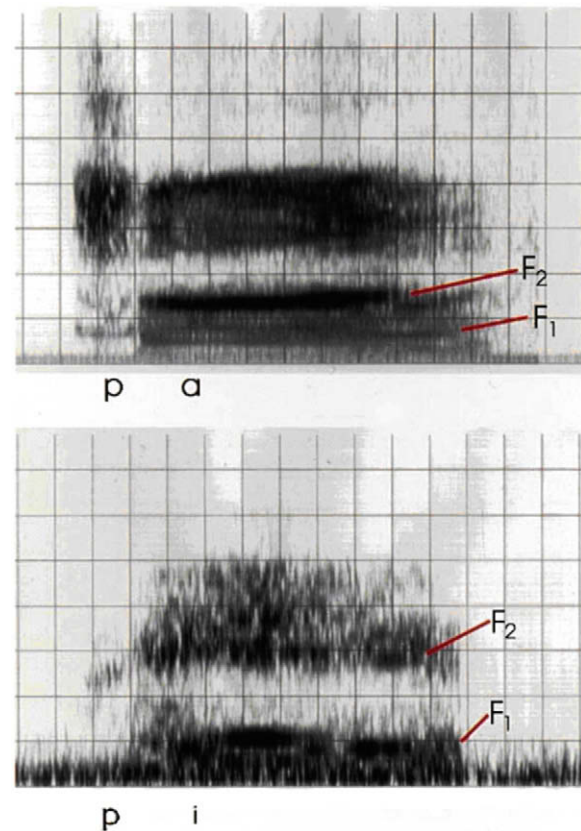


Fig. 1. Alex's production of "pah" /pa/, his label for pasta and for "pea" /pi/, his label for a green pea.

Greys (Klatt & Stefanski, 1974). Budgerigars produce human vowels by amplitude modulation, but not quite as Lieberman suggests. Because their syrinx cannot produce two independent sounds, they produce speech via a different, as yet undetected, mechanism (Banta Lavenex, 1999).

2.2.2. Vowels— F_1 and F_2 analyses

Accurate production of human speech involves formants, resonant frequencies of the human mouth opening (F_1) and oral cavity (F_2) that could also represent specific parrot vocal tract areas; sometimes F_3 is necessary (Borden & Harris, 1984; Lieberman, 1984). A formant is not a harmonic of F_0 ; harmonics, if present, appear as odd multiples of F_0 . F_1 and F_2 variations may differentiate vowels for classes of human speakers. We compared Alex's and my F_x 's and tested whether Alex's formants predict his vowels (Patterson & Pepperberg, 1994). For both F_1 and F_2 , his range was smaller than mine and lacked my low frequency values. His F_1 s, which in humans roughly corresponds to tongue height, differed considerably from mine and, unlike mine, varied little across most vowels (Warren et al., 1996). Our F_2 s, which in humans corresponds to front/back tongue position, were similar: Like mine, his vowels were somewhat distinguishable by F_2 ; his front/back position varied considerably. Thus, as for humans, his formants correlated with specific vocal tract area resonances (Beckers, Nelson, & Suthers, 2004; Remez, Rubin, Nygaard, & Howell, 1987; Warren et al., 1996). His F_3 s, which in humans indicate whether speech-producing constrictions occur toward the front or back of the vocal tract, were rarely observed or nearly indistinguishable from F_2 . All his vowels clustered in the high/low midrange but his /i, I, E, ae/ and /U, ə, a/ respectively cluster as 'front' and 'back' vowels. /u/ is a back vowel for most Standard American English

speakers; for Alex and me it was a diphthong—had two parts, /u₁/ and /u₂/. Mine are front vowels; Alex's were front and back vowels, respectively (Patterson & Pepperberg, 1994).

2.2.3. Stop consonants

Traditional acoustic analyses for stops (consonants with blocked air flow) generally applied to Alex (Patterson & Pepperberg, 1998). We examined voice-onset timing (time for humans between lip opening to release air and start of sound source vibration), number of bursts (bursts result from release of air pressure built up by lip closure), and stop loci (high energy peaks associated with voiceless aspirated portions of stops). We measured formant frequency in the first 10 ms of voicing following a stop, average formant frequency during the steady state portion of a vowel following a stop, and time from beginning of voicing to when formants assume a steady state pattern. Similarities and differences exist for our stops (Patterson & Pepperberg, 1998). Similarities involve statistically distinct acoustic characteristics and separation of stops into voicing and place of constriction subsets. Differences involve specific subset divisions and mechanisms for /b,p/ production. Compared to my subsets, Alex's /b/ was an outlier; his /p/ clustered nearer /d,g/ than /t,k/. Alex produced bilabial /b,p/ without lips; unlike normal humans, he likely used esophageal involvement (Patterson & Pepperberg, 1998).

2.2.4. Related data

X-ray video data (Warren et al., 1996) suggest that Alex used anticipatory co-articulation, setting up his vocal tract for the next speech sound as the previous one was completed (e.g., his /k/ in “key” differs from that in “cork”, Patterson & Pepperberg, 1998). Thus he appeared to separate specific phonemes from the speech flow and produce them so as to facilitate production of upcoming phonemes. In humans, these abilities are taken as evidence for top-down processing (Ladefoged, 1982), and are necessary for segmentation and phonological awareness, discussed below.

Alex's reproduction of human speech was likely constrained only by human–avian vocal tract differences (e.g., no lips). His vocalizations all resemble human samples; characteristics that describe human speech and processes used to produce human speech apply to him (Patterson & Pepperberg, 1994, 1998). *F₀* data specifically show that Alex, like humans, produces true resonances, not sinusoids at appropriate formant frequencies. His brain areas devoted to vocal learning (Jarvis, 2004) control numerous vocal tract areas in order to produce human speech, a form of gestural learning (Arbib, 2005). Such data relate to gestural theories of song and language evolution, to mirror neurons (MNs, neurons that respond the same way whether one performs or views an action), and to mirror neuron systems (MNS; e.g., Arbib, 2005).

2.3. Mirror neurons

Gestural (or motor) theories of language and song evolution suggest how vocal communication evolved in, respectively, primate (Hewes, 1973) and avian lines (Williams & Nottebohm, 1985). A very brief summary of rather complex ideas is that (a) manual gestures—possibly accompanied and modified by grunts or calls—shifted to vocal tract—articulatory—gestures that supported finer-grained vocal communication and (b) an individual understands and acquires vocal communication by representing the speech that is heard as motor articulatory behavior (Lieberman & Mattingly, 1985; Vihman, 1993), which can then be both interpreted and reproduced. Such representation and acquisition is assisted if, for example, your articulatory system responded to my voice as if you were talking. Interestingly, some MNs involve exactly that parity (e.g., Arbib, 2005; Craighero, Buccino, & Rizzolatti, 2002). And, because MNs have an inhibitory component, allowing

you not to repeat my utterance if you so chose (Baldissera, Cavallari, Craighero, & Fadiga, 2001), they do not preclude voluntary action. The specific connection to language is that MNs are found in Broca's area—one of the human ‘language centers’—and in the monkey analogue of Broca's area, F5; the monkey's system and part of the human system both react to manual grasping and related actions (e.g., Fadiga, Fogassi, Pavesi, & Rizzolatti, 1995), including ‘mouthing’ actions in monkeys and articulatory actions in humans (Craighero et al., 2002). As hypothesized by Rizzolatti and Arbib (1998), the development of vocal from manual communication involves evolution of Broca's area from F5: no longer would speech require a major brain reorganization, only reorganization of the MN system from voluntary control of manual gestures to include articulatory ones (e.g., Corballis, 2003), so as to handle the evolution of *learning* to communicate. Various types and levels of MN systems likely exist, both across and within species. Notably, monkeys, unlike humans, fail to engage in vocal learning or even true manual imitation (Visalberghi & Fragaszy, 1990) but have intact MN systems. Even in humans, MN systems possibly vary developmentally or with respect to control of various levels of behavioral complexity (e.g., Pepperberg, 2006). Similarly, brain structures responsible for avian unlearned calls could have evolved to control suboscines' unlearned songs, then to control the complex learned oscine system and parrots' open-ended learning (Faries, 2001; Pepperberg, 2006). But until recently, mammalian–avian parallels were unclear.

Certain avian and mammalian brain structures, including those responsible for vocal learning, are now thought to have evolved from the same reptilian pallial structures (Jarvis et al., 2005); thus it does not seem unreasonable to propose some form of avian MN system. One cannot, however, argue for direct correlations to Broca's area in birds as one can for F5 in monkeys. Possibly the bits of brain corresponding to specific mammalian language/articulatory gesture centers are apportioned across several song centers in the avian brain (Reiner, pers. comm., April 19, 2005; see Jarvis, 2004; also Kirn, this volume, for discussions and definitions of songbird brain circuitry).¹ Interestingly, for the oscine song sparrow, Prather, Peters, Nowicki, and Mooney (2008) found HVC_x neurons (a population of neurons in the songbird HVC, the higher vocal center—necessary for the learning and *production* of song—that innervates Area X, another brain area important to song learning and *perception*) that display nearly identical patterns of activity when a bird sings and hears the same sequence of notes. Although the authors are careful not to claim that these neurons are indeed MNs, and suggest that the exact MN system could lie downstream (e.g., as part of a loop involving other song areas), the involved brain areas do correlate with those involved in human vocal behavior. Given our knowledge of parallels among songbird, human, and parrot vocal centers (Jarvis et al., 2005), a comparable parrot MN system is likely. Because parrots lack a specific correlate to HVC_x, quite possibly the MN-related area is indeed downstream for both parrots and songbirds, or also involves connections between what are parrot correlates of songbird areas: i.e., connections between AAC (nucleus centralis arcopallii anterioris) and MMSt (magnocellular nucleus of the medial striatum), the parrot versions, respectively, of RA (robust nucleus of the arcopallium, part of the song *production* pathway) and Area X (the *perception* area noted above). The parrot system also likely differs somewhat from that of most songbirds so as to allow for more diverse forms of imitation. Specifically, given studies demonstrating how, in adult songbirds, LMAN (lateral magnocellular nucleus of the nidopallium) inactivation reduces singing variability (Kao, Doupe, &

¹ Arguments also exist, of course, that what some researchers consider specific language modules are actually more like bottlenecks in distributed networks connecting various populations of neurons necessary for communicative behavior; see review in Scharff & White (2004); note also Liberman and Mattingly (1985).

Brainard, 2005; Ölveczky, Andalman, & Fee, 2005) and the connections in songbirds between X, LMAN, and RA for perception and production, quite likely in parrots the MNS for imitative behavior will involve NAOc (the oval nucleus of the anterior nidopallium complex)—which is the parrot equivalent of LMAN—and its connections to MMSt and AAC. Interestingly, cross-species MN responses are already documented: Monkey F5 MNs respond to human hand gestures; might some form of parrot MNs involved in articulatory gestures respond to those of humans and assist with psittacine learning of human speech?

3. Cognitive capacities and vocal learning

Studies of perception, production, and even MNs address parrots' physical abilities, but not the extent and processes of their vocal learning. Parrots, unlike most songbirds, are open-ended learners; moreover, many parrots master allospecific acquisition. This trait, observed in nature (Cruickshank et al., 1993), is most obvious in captivity. And, although many captive parrots may mindlessly mimic Greys, at least, can learn to use human speech referentially (Pepperberg, 1981, 1999). What appears to enable reference is the form of training.

Parrots do not readily acquire any novel sound. Pet birds may indeed mimic random utterances and environmental noises without apparent instruction, but fail to learn English speech via psychological conditioning techniques (e.g., Grosslight & Zaynor, 1967; Mowrer, 1950; Pepperberg, 1999). Thus, for parrots, different types of vocal learning likely require different types of input: Simple mimicry used only to attract attention differs from acquisition of vocalizations having communicative content (Pepperberg, 2002). Like young children (e.g., Hollich, Hirsh-Pasek, & Golinkoff, 2000), Greys acquire communication skills most effectively when teaching is referential, functional, and socially rich (Pepperberg, 1997, 2004). Reference is an utterance's meaning—the relationship between labels and objects to which they refer—and is exemplified by presenting to the bird, during training, the specific objects being named, as the primary reward for vocalizing appropriately. Functionality involves the context and effects of an utterance's use; opportunities during training for using labels to request objects provide a rationale for learning unique, unfamiliar sets of sounds constituting human speech. Social interaction between subject and trainer focuses attention on certain aspects of the environment, emphasizes common attributes of objects or actions (and possible underlying rules for their use) and allows trainers to adjust procedures to a learner's level. Interaction with trainers engages subjects directly, provides a contextual explanation for actions, and demonstrates the consequences of those actions (Pepperberg, 2004). These elements of training define what has become known as the model/rival technique.

3.1. The model/rival (M/R) technique

In the 1970s, after reviewing what was then known about parrots' vocal learning, child language acquisition, and human social learning, I devised the M/R procedure to teach parrots referential use of human speech (Pepperberg, 1981). M/R training, based on methods developed by Todt (1975) and Bandura (1971), uses three-way social interactions among two humans and a parrot to demonstrate the targeted vocal behavior (Pepperberg, 1981). The parrot watches and listens as one trainer presents objects and queries the other trainer about them (e.g., "What's here?", "What color?"), giving praise and transferring the named object to the human partner to reward correct answers. Incorrect responses are punished by scolding and temporarily removing items from sight. Thus the second human is both a model for the parrot's re-

sponses and its rival for the trainer's attention, and illustrates consequences of errors. The model must try again or talk more clearly if the response was deliberately incorrect or garbled; that is, the model is subject to corrective feedback, which the bird observes. The parrot is included in interactions, being queried and rewarded for successive approximations to correct responses; training is adjusted to its performance level. If a bird is inattentive or accuracy regresses, trainers threaten to leave.

Unlike M/R procedures others have used (see Pepperberg & Sherman, 2000), ours exchanges roles of trainer and model. The parrot thus sees how questioner and respondent interchange roles, and how the procedure causes environmental change. Role reversal also counteracts an earlier methodological problem: birds whose trainers always maintained their respective roles responded only to the human questioner (Todt, 1975). With our system, birds respond to, interact with, and learn from any human.

To ensure the closest possible link between labels or concepts to be learned and their appropriate referent, M/R training uses only *intrinsic reinforcers*: reward for uttering "X" is X, the object to which the label or concept refers. Earlier unsuccessful attempts to teach birds to communicate with humans used *extrinsic* rewards: a single food that neither related to, nor varied with, the label or concept being taught (Pepperberg, 1999). This procedure delayed label and concept acquisition by confounding the label of the targeted exemplar or concept with that of the food reward. Initial use of labels as requests also demonstrates that uttering labels has functionality; later, birds learned "I want X", to separate requesting and labeling (Pepperberg, 1988) and to enable them to request preferred rewards while learning labels for items of little interest to them.

M/R training successfully enabled label and concept acquisition (for Alex's repertoire, see Pepperberg, 1999), but did not specify which training elements were *necessary and sufficient*. Earlier unsuccessful attempts to teach birds referential speech lacked at least some of these elements but neither deconstructed the learning environment nor tested the significance of different input elements individually and in various combinations. To learn why M/R training was so successful, and whether some subset of input elements would suffice, I began testing how changes might affect learning not only with respect to sound reproduction, but also with respect to comprehension and appropriate use, focusing on actions that require cognitive processing.

3.2. Eliminating aspects of M/R training

To provide training input that varied in amounts of reference, functionality, and social interaction, I contrasted M/R tutoring with sessions using audiotapes, videos, and different levels of human interaction; I also involved additional subjects. Had I significantly changed Alex's training protocols, he might have ceased learning simply because I had made a change, not because of the quality of the change. New subjects, lacking training, would not be influenced by prior experience. I performed one M/R variant with Alex and more extensive permutations with four naïve Greys: Kyaaro, Alo, Griffin, and Arthur.

The juveniles Alo and Kyaaro experienced sessions in social isolation (Pepperberg, 1994b): Each heard audiotapes of Alex's sessions (input now nonreferential, not contextually applicable, and non-interactive) and saw videotapes showing how Alex and trainers received referential rewards for labeling (input now referential, non-interactive, minimally functional and contextually applicable). Nothing the juveniles uttered could enable reward. In all cases, no new labels were acquired; however, both birds learned referential labels in concomitant M/R sessions, showing that the birds' abilities were not the issue.

Additional experiments explored video-training variations (Pepperberg, Gardiner, & Luttrell, 1999; Pepperberg, Naughton, & Banta, 1998; Pepperberg & Wilkes, 2004). First, a co-viewer provided social approbation for viewing and pointed to the screen while making comments like “Look what Alex has!” but did not repeat targeted words, ask questions, or relate content to other training. Birds’ attempts to utter a label could garner only vocal praise; social interaction was limited; referentiality and functionality matched earlier video sessions. Second, the co-viewer was more interactive, uttering targeted labels and querying birds. Third, a socially isolated parrot watched videos while a student in another room monitored its utterances via headphones and could deliver intrinsic rewards remotely. Fourth, we used live video from Alex’s sessions to minimize habituation. Fifth, in a study with Arthur, using an LCD monitor, we tested whether CRT screen flicker could affect learning. Birds did not learn labels from any of these procedures, but, again, learned labels presented in concurrent, traditional M/R sessions.

Based on studies with children (Baldwin, 1991), I examined the role of joint focusing of attention between bird and trainer. A single trainer faced away from a bird, who was within reach of, for example, a key; the trainer talked about the object, emphasizing its label, “Look, a shiny key!” “Do you want key?” etc. These sentences framed the label, allowing for repeated label use while minimizing possible habituation (Pepperberg, 1981). The trainer had no visual or physical contact with the parrot or object. If a bird attempted to utter the targeted label, it would receive vocal praise. Overall, some functionality and considerable social interaction were eliminated (Pepperberg & McLaughlin, 1996). Again, no new label learning occurred.

An experiment with Griffin eliminated the second trainer. One student labeled objects to which she and Griffin jointly attended (Pepperberg, Sandefer, Noel, & Ellsworth, 2000). Griffin did not utter any targeted label during or immediately after 50 such sessions, but did so after two or three subsequent M/R sessions involving the same items. Because birds switched to M/R training after 50 video sessions needed about 20 sessions before beginning to acquire targeted labels (Pepperberg, 1999)—about the same number of sessions needed when labels are introduced initially in M/R training—Griffin had likely acquired labels during the solo-trainer sessions, but did not understand how to use them until he observed their usage modeled. Importantly, he learned new labels and their use in concurrent M/R sessions with other objects.

Learning that occurs with impoverished input may produce mimetic speech, as in Alex’s M/R-variant study, where I eliminated as much reference and functionality as possible while retaining a two-trainer system (Pepperberg, 1994b). Alex viewed a string of pictured Arabic numerals as two humans interacted: the model/rival stating “Say number”, the other uttering a vocal sequence based on Korean count labels, but without reference either to specific numerals or to Alex’s previously acquired English number labels (Pepperberg, 1994a, 1997). The Korean-based labels, required for a simultaneous study on serial learning (Silverstone, 1989), provided maximal contrast with English. Training lacked functional meaning and all but minimal referentiality—the page with numbers was simply a focus for joint attention. As in the basic M/R procedure, roles were reversed and Alex was included in interactions. Reward was the opportunity to request a favored item (“I want X”) and vocal praise; errors elicited scolding and time-outs.

Alex learned the string of modeled vocal labels—but results differed from those of M/R studies (Pepperberg, 1981, 1994b; Silverstone, 1989). Strikingly, he did not use these sounds as labels, nor could he subsequently learn to use them referentially—that is, with respect to either serial labeling or quantity, even after we paired them with objects as one would state “first, second, . . .”, etc. Alex had thus learned to produce, but apparently could not learn to

comprehend, these sounds (Pepperberg, 1994b), like a child who, having learned the ‘alphabet song’ thinks ‘LMNOP’ is one letter (Pepperberg, 2004). Given his previous success on label production and comprehension after M/R training (e.g., Pepperberg, 1990a, 1990b, 1992, 1994a), Alex’s failure was likely a consequence of the training protocol (Pepperberg, 1994b). Thus referential imitation differs from ‘mere mimicry’, and training that engenders the latter is usually incapable of engendering the former, with the implication that different cognitive processes—and possibly different neural areas (e.g., see below: separate or different levels of MN systems; Pepperberg, 2006)—are involved in the two situations.

In sum, Grey parrots apparently acquire referential speech only via original M/R training. Training must involve two humans who demonstrate referentiality and functionality of a label to be learned, who socially interact with each other and the bird, exchange roles of questioner and respondent, portray the effects of labeling errors, provide corrective feedback, and adjust the level of training as the subject begins to learn. When training lacks some or all of these elements, birds typically fail to learn referential speech.

Similarities exist with respect to the importance of social interaction for vocal learning in many species. Without going into detail, I note that songbirds given impoverished input—audiotapes in sound isolation boxes (Marler, 1970)—demonstrate limitations not observed in nature, for example, on the period during which they can learn song and their capacity for allospecific and conspecific (multiple dialect) acquisition (see Baptista & Gaunt, 1997). Birds given live tutors, in contrast, may extend the song acquisition period and learn songs of allospecific, sympatric species (Baptista & Gaunt, 1997). Dolphins also exhibit more rapid and flexible vocal learning when exposed to procedures that are referential and functional (Reiss & McCowan, 1993) compared to operant techniques (Richards, Wolz, & Herman, 1984), and preliminary evidence exists for some level of social allospecific learning in elephants (Poole, Tyack, Stoeger-Horwath, & Watwood, 2005). Children who experience labeling that lacks joint reference fail to acquire targeted labels (Baldwin, 1991) and children who watch videos in isolation learn less than children with interactive trainers (e.g., Rice, Huston, Truglio, & Wright, 1990). Children who have developmental communicative disabilities also learn more in model/rival situations than with procedures that lack various elements of M/R training (see Pepperberg & Sherman, 2000, 2002).

Specifically, Grey parrots’ *simultaneous* acquisition of sound patterns and their association with specific objects during M/R training argue for a mechanism different from simple mimicry, as do data showing the difficulty of training label-object associations after mimetic label acquisition for Greys, apes, and dolphins (Pepperberg, 1999). Note, too, data (below) suggesting that, as Alex matured, he began constructing novel labels not by directly reproducing his human trainers’ speech but by composition from existent labels (and segmented parts of existent labels) in his repertoire.

4. Developmental similarities with children and songbirds: untrained vocal practice

Like children (e.g., Kuczaj, 1983; Nelson, 1989) and songbirds (e.g., Baptista, 1983; Marler, 1970), Alex engaged in active vocal practice before acquiring targeted vocalizations. Using sound play (phonetic ‘babbling’/recombination; Pepperberg, Brese, & Harris, 1991) he derived new speech patterns spontaneously from existent ones. After acquiring “grey”, for example, he produced sound variants that we eventually mapped to appropriate referents (Pepperberg, 1990c; see below). Notably, these recombinations suggest he abstracted rules for utterances’ beginnings and endings. In over

22,000 vocalizations, he never made backwards combinations (e.g., “percup” instead of “cupper/copper”; Pepperberg et al., 1991). As noted above, he seemed to exhibit anticipatory co-articulation; such behavior observed along with sound play is often considered evidence for top-down processing (Ladefoged, 1982). Finally, he engaged in label segmentation in a manner suggesting some form of phonological awareness (Pepperberg, 2007, 2009). I discuss all but co-articulation in some detail.

4.1. Vocal play

Sound play—repetitions and variations on vocal patterns—has many forms, including “monologue speech”: active practice of a communication code in situations without overt social stimulation (Kuczaj, 1983). Monologue speech further divides into *private speech* produced in solitude and *social-context speech* produced in the presence of potential receivers but lacking obvious communicative purpose. When alone in his cage, Alex engaged in the former, which explained some of his acquisition data: Although most of his labels appeared initially as rudimentary patterns that improved during training—first as a vocal contour, then with vowels, finally with consonants (Patterson & Pepperberg, 1994, 1998)—sometimes completely-formed new labels or entire phrases materialized after minimal training and without practice in his trainers’ presence. By eavesdropping, we found he was practicing these utterances privately (Pepperberg et al., 1991).

Such behavior patterns are presumably integral to development; their occurrence across species (e.g., songbirds (Marler, 1970); children (Nelson, 1989; Weir, 1962); cetaceans (McCowan, Hanser, & Doyle, 1999)), suggests an evolutionary theory of language play (Kuczaj, 1998). Like most play, monologue speech facilitates learning by allowing experimentation with adult systems: full freedom to choose topics and contexts, to attempt novel words, and compare familiar and novel forms to extract regularities and discover differences (Kuczaj, 1983). Lack of negative feedback or the need to use correct forms may encourage practice and even accelerate learning.

Equally important for repertoire expansion, Alex’s social-context speech appeared when, with trainers nearby, he produced new vocalizations by recombining existing label parts in their corresponding orders (Pepperberg, 1990c). Such spontaneous novel phonemic combinations often occurred outside of testing and training, and juvenile Greys behave similarly (e.g., Neal, 1996; Pepperberg, 2004), with combinations appearing in contexts and forms reminiscent of children’s play. These utterances were rarely if ever used by trainers, but sometimes resembled both existing labels and separate human vocalizations (e.g., “grain” from “grey”). When we *referentially mapped* these spontaneous utterances—providing relevant objects to which they could refer—Alex rapidly integrated these labels into his repertoire. For “grain”, trainers gave Alex seed, something not normally available; later sprouted legumes were substituted. He received a paper clip ring for “chain”, appropriate fruit for “grape”, and a nutmeg grater for trimming his beak after uttering “grate”. “Cup” (from “up”) was rewarded with metal cups and plastic mugs, “copper” (first produced as “cupper”) with pennies, and “block” with cubical wooden beads. “Chalk” (from “talk”) mapped to blackboard chalk; “truck” to toy cars and trucks. We ignored “shane” and “cheenut”; he abandoned these sounds (Pepperberg, 1990c). Thus Alex’s spontaneous utterances that initially lacked communicative value could, as they do for children, acquire such value if caretakers interpreted them as meaningful and intentional (Pepperberg, 1990c); he behaved as though our interactions “conventionalized” both the sound patterns and the sound-meaning connections in the direction of standard communication.

Somewhat like children engaged in testing meanings of newly-acquired labels (e.g., Brown, 1958, 1973), my birds also use humans to provide additional referential information for relatively novel labels (Pepperberg, 2002). Our youngest subject, Arthur, uttered a label used in a very specific context—“wool”, for a woolen pompon—while pulling at a trainer’s sweater. He seemed to be testing the situation, and our responses—given with high positive affect—stimulated him further, revealing the potential power of an utterance and encouraging his early categorization attempts. Even if birds err in initial categorizations, they are reinforced when we provide a correct, new label for the item: replying that an almond isn’t “cork”, but “cork nut”—a label they will subsequently use (Pepperberg, 1999, 2002).

4.2. Segmentation

Of even greater interest is that Alex appeared capable of vocal segmentation—a special form of vocal combinatory behavior—that (a) implied that he understood that his existent labels were formed of individual morphemes or phonemes that could be combined in novel ways to create what were for him novel vocalizations (e.g., Greenfield, 1991; Peperkamp, 2003), and (b) would also demonstrate phonological awareness (Pepperberg, 2007). Such behavior is not only considered basic to human language development (Carroll, Snowling, Stevenson, & Hulme, 2003), but also a uniquely human trait: most animals, lacking speech, are never exposed to, nor trained nor tested on, phonological awareness, nor are they expected to have internal representations of phonemes that would engender such combinatorial behavior (Pepperberg, 2007). Such behavior is not innate even for humans: Children apparently shift from recognizing and producing words holistically (Studdert-Kennedy, 2002) to recognizing words as being constructed via a rule-based phonology when about three years old (Carroll et al., 2003; Vihman, 1996); furthermore, manipulation of individual parts of words is presumed to require development of an internal representation of phonological structure (Byrne & Liberman, 1999). That is, in order to sound out—rather than mimic—a novel label, children must segment the sound stream into discrete elements, recognize a match between those elements and elements (or close approximations) in their own repertoires, and then recombine these elements into an appropriate sequence (see Gathercole & Baddeley, 1990; Treiman, 1995). Moreover, children’s ability to focus on the sounds of words and sound elements of words rather than solely on word meaning may be assisted by training in sound–letter associations (Carroll et al., 2003; Mann & Foy, 2003). Little evidence exists for segmentation in animals, even a less advanced form involving combination and/or recombination of whole labels to describe novel situations. The few existent incidents—apes’ “water bird” for a swan, “cry hurt food” for a radish (Fouts & Rigby, 1977), dolphins’ “ring–ball” during simultaneous play with two items (Reiss & McCowan, 1993)—have been considered as descriptors of the entire situation rather than as specific combinations to denote one element. The following data present evidence for segmentation by Alex (Pepperberg, 2009).

After observing the attention that Arthur received for labeling a wooden bobbin as “spool” (Fig. 2A), Alex evinced interest in the item, and received M/R training to produce the label. For spool, unlike his usual form of acquisition, Alex began using a combination of existing phonemes and labels to identify the object: /s/ (unvoiced, trained in conjunction with the alphabet letter, S) and wool, to form “s” (pause) “wool” (“s-wool”; /s-pause-wU/; see Fig. 3; Pepperberg, 2007). The pause seemed to provide space for the absent (and difficult) /p/ (possibly to preserve the number of syllables or prosodic rhythm of the targeted vocalization; see Leonard, 2001; Peters, 2001). None of Alex’s prior labels contained /sp/, nor did his repertoire include “pull” or “pool”, nor any label including /ul/. He

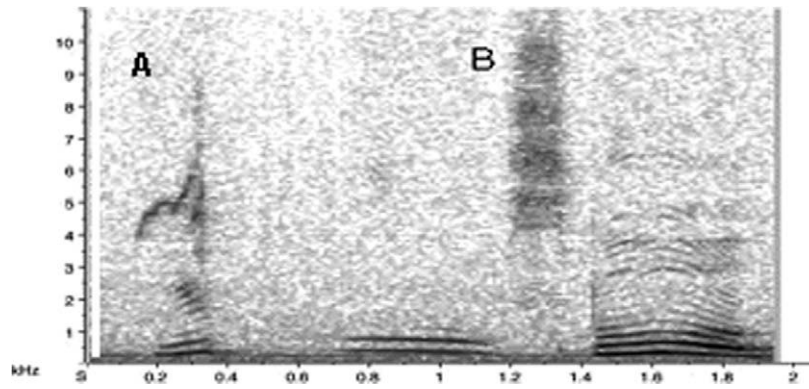


Fig. 2. (A) Arthur's "spool" compared to (B) Pepperberg's "spool" (from Pepperberg, 2007).

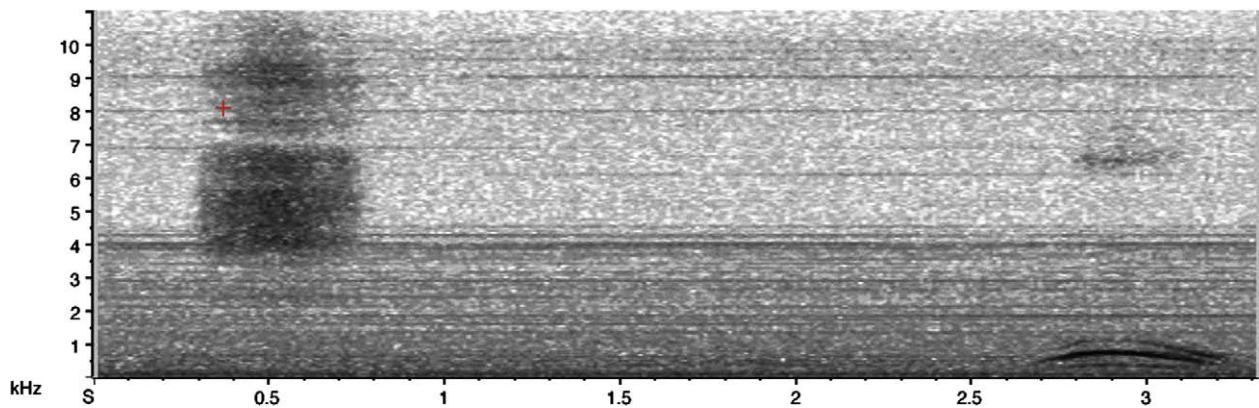


Fig. 3. Alex's "s-wool" (/s-pause-wU/) (from Pepperberg, 2007).

knew "paper", "peach", "parrot", "pick", etc. and "shape" and "sich" (six); technically, /p/, /sh/ and /s/ but not /sp/ were available. He knew /u/ from labels such as "two" and "blue" (Pepperberg, 2007). Note that both Alex's and my /p/, when analyzed for VOT (voice onset time), fall solidly into the voiceless category, distinct from the voiced /b/ (Patterson & Pepperberg, 1998).

Alex retained "s-wool" for almost a year, even though usually only several weeks of training enable learning of a new label with existent phonemes (Pepperberg, 1999). After this year-long period, he spontaneously produced a perfectly formed "spool" (/spul/), replacing the space with /p/ and shifting the vowel to /u/ from /U/ (see Figs. 4 and 5; Pepperberg, 2007). His utterance sounded distinctly human, differed from Arthur's whistled version, and

clearly resembled mine (Figs. 2B and 5C), even though students had performed 90% of the training.

Whether Alex's shift from /U/ to /u/ was gradual is unknown. Unlike a previous laboratory situation in which Alex was alone for specific periods each day to enable eavesdropping on his solitary practice (Pepperberg et al., 1991), three birds (Alex, Griffin, Arthur) were now together 24/7. A gradual shift was unlikely if Alex had maintained his previous pattern of vocalizing in private: Significant portions of Alex's solitary practice involved what in humans would be considered rhymes (e.g. "green, cheen, bean"; "mail, banail") in which ends of labels were stable (Pepperberg et al., 1991); that is, he seems to have (or have acquired) categorical distinctions and minimal pairs similar to those of his human

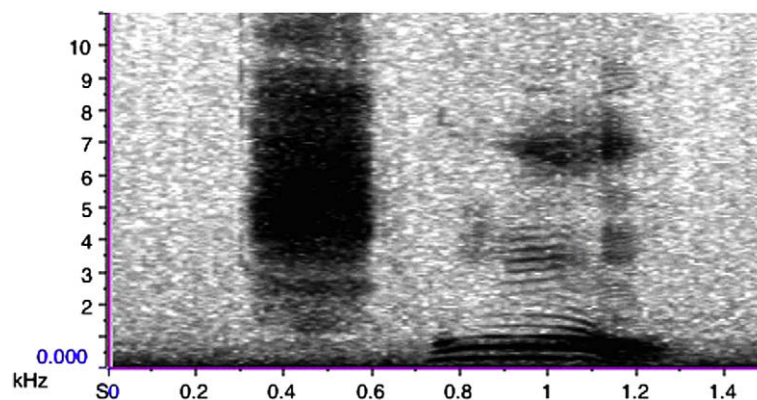


Fig. 4. Alex's "spool" (/spul/) (from Pepperberg, 2007).

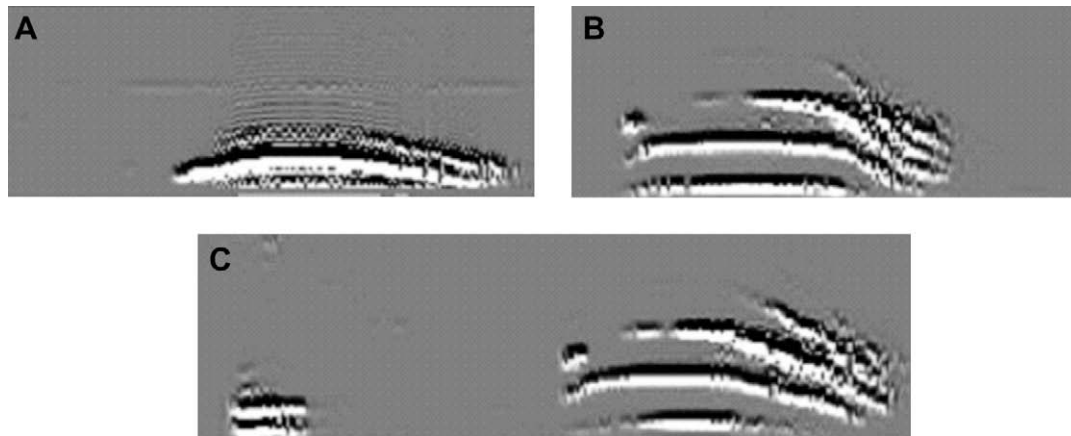


Fig. 5. (A) Alex's /U/; (B) Alex's /u/, (C) part of Pepperberg's /spu/ (from Pepperberg, 2007).

models (Patterson & Pepperberg, 1994, 1998). An abrupt shift could indicate some level of self-monitoring and even some additional awareness that the appropriate vowel for “spool” derived from yet another label such as “two” (/tu/); such information was unavailable to Arthur (Pepperberg, 2009).

The pattern of acquisition is not unique to “spool”; Alex exhibited a similar pattern for the vocalization “seven” (first in reference to the Arabic numeral, then to an object set). Alex's first production of the label could best be described as “s...n”, a bracketing using the phonemes /s/ and /n/; he then quickly progressed to “s-one” (see Fig. 6; /s/-pause-wən/) which looked quite different from my “seven”, but followed the form of “s-pause-wool”.

Eventually, he replaced “s-one” with something sounding to the human ear like “sebun”, much closer to my “seven” (Fig. 7; sonograph expanded for reference).

Alex's training likely enabled him to use phonological awareness (in the sense defined in Anthony & Francis, 2005) to create a difficult new label from existing bits of sounds already in his repertoire (i.e., via segmentation) and to carefully produce the appropriate phonemes. As presented above, Alex's data demonstrate that

he had a functional understanding that his existent labels were comprised of individual units that could intentionally be recombined in novel ways to create referential, novel vocalizations (Pepperberg, 2007). Although Alex seemingly generated novel meaningful labels from a finite set of elements, the rule system he demonstrated was relatively limited. Nevertheless, the data add another intriguing parallel between Alex's and young children's early label acquisition.

4.3. Neural correlates

Notably, the different vocal behaviors discussed above might involve different neural mechanisms or combinations thereof. That is, Alex's social-context speech, in which he generated vocal variability—without necessarily having a specific targeted outcome—might be neurally different from practice or segmentation in which he appeared to actively compare auditory production with a stored template in an attempt to produce a specific label.

Ólveczky et al. (2005) and Aronov, Andalman, and Fee (2008) have shown that juvenile songbirds' LMAN is involved in generat-

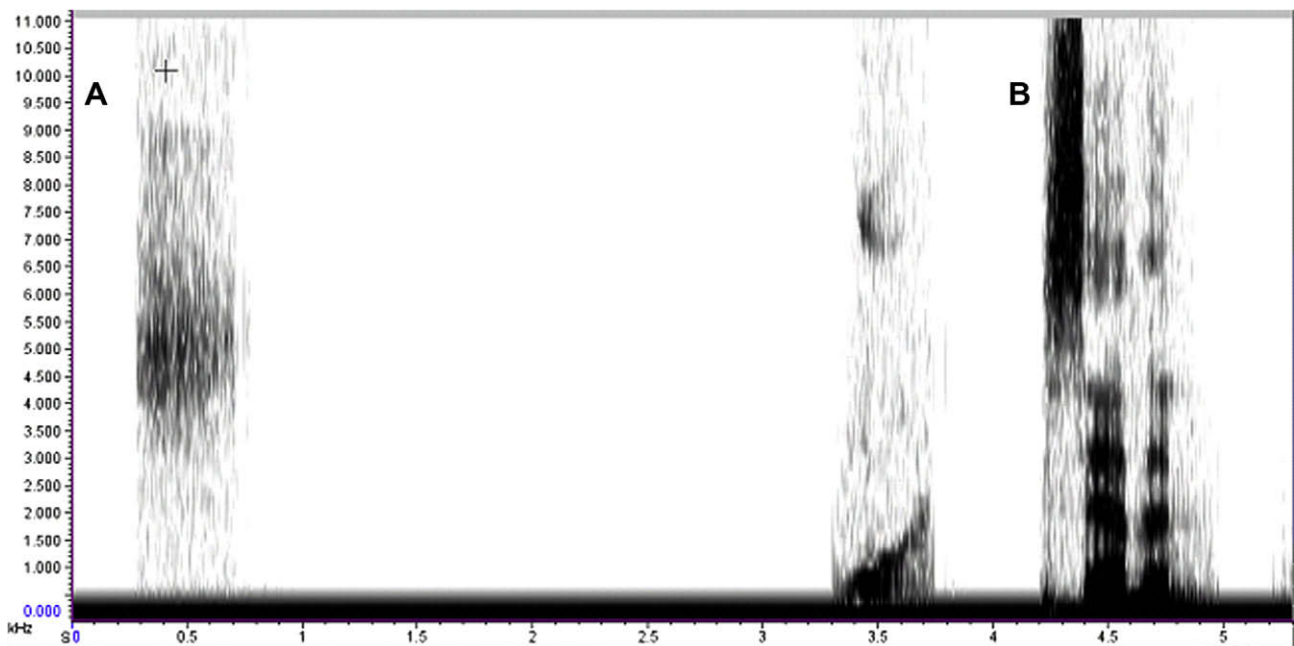


Fig. 6. (A) Alex's “s-one” /s/-pause-wən/ followed by (B) Pepperberg's “seven” /sEvIn/ (from Pepperberg, 2009).

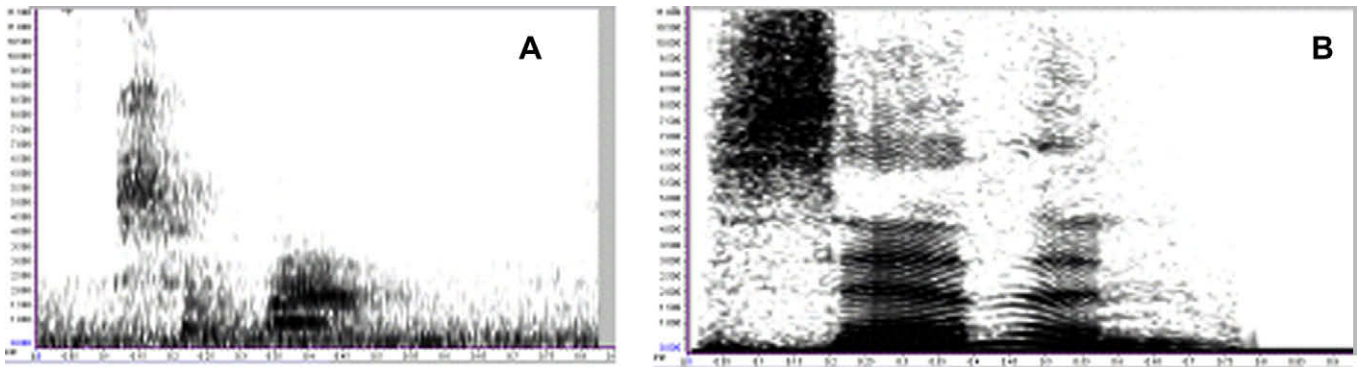


Fig. 7. (A) Alex's "seven" [/sEbIn/] compared to (B) Pepperberg's "seven" [/sEvIn/] (from Pepperberg, 2009).

ing extreme vocal variability across song renditions, a behavior that enables exploration of a range of possible patterns from which birds will home in on those that match a specified type of input. Lesioning LMAN prevents juvenile birds from expressing variable patterns, resulting in aberrant, stereotypic final vocalizations. Lesioning LMAN in adult songbirds, in contrast, has little effect on song production other than reducing some stereotypy (Doupe, Solis, Kimpo, & Boettiger, 2004; Kao et al., 2005). As noted earlier, in open-ended learning parrots, their area NAOc—corresponding to LMAN—might remain active throughout life and be responsible for Alex's ability to generate a vocal series such as "grey" → "grate" → "grain" → "chain" → "cane". Here, Alex did not appear to have specific goals; he vocalized spontaneously and the vocalizations were mapped to meaning through actions of his human trainers (rewards).

But what happens when there was a goal, as in Alex's production of "spool" or "seven"? Here, Fiete, Fee, and Seung (2007) propose an intriguing model in songbirds that could similarly be adapted for parrots, and could also tie into the MN system suggested earlier. A very simplistic description of the Fiete et al. model is that if a particular coincident input (out of many possibilities) to RA from LMAN and HVC_{RA} is followed by some form of reinforcement (unspecified as to origin), the output from RA leads to what corresponds to crystallized song. Interestingly, however, HVC_x neurons (those proposed as possibly connected to an MN system) but not HVC_{RA} neurons respond robustly to bird's own song (Prather et al., 2008), and HVC_x neurons may trigger LMAN activity through disinhibitory mechanisms (see Mooney, 2004; note Doupe et al., 2004). Although considerable work remains to determine specific details of which avian brain area determines when the output is 'correct' and how this mechanism functions, some integration of pathways including MN systems must exist for iterative learning in songbirds along with a corresponding parrot loop involving NAOc, AAC (the RA correlate in parrots), and NLC (the nidopallial vocal nucleus correlate of HVC in parrots). A caveat is that no equivalent HVC_x connection exists in parrots (Jarvis, 2004), but rather AAC to NAOc (what would be RA to LMAN in songbirds), and NAOc to NCL instead. Likely Alex's slow, deliberative matching of vocal output to specific human labels involves such an iterative neural pathway, in contrast to the rapid variations produced in his vocal play.

5. Summary

Vocal learning is rare, but exists in species that are phylogenetically distant, even within the avian (songbirds, parrots) and mammalian (humans, cetaceans, elephants) lines. Similarities exist among vocal learners, not only in their ability to learn a vocal code, but also often in the manner in which the code is acquired. Striking

parallels exist particularly within the human and Grey parrot system, suggesting that birds, and particularly parrots, are appropriate models for studying the evolution not only of vocal communication, but also of vocal learning (Pepperberg, 2009).

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