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Vocal learning of a communicative signal in captive chimpanzees, *Pan troglodytes*

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Abstract

We hypothesized that chimpanzees could learn to produce attention-getting (AG) sounds via positive reinforcement. We conducted a vocal assessment in 76 captive chimpanzees for their use of AG sounds to acquire the attention of an otherwise inattentive human. Fourteen individuals that did not produce AG sounds during the vocal assessment were evaluated for their ability to acquire the use of an AG sound through operant conditioning and to employ these sounds in an attention-getting context. Nine of the 14 chimpanzees were successfully shaped using positive reinforcement to produce an AG sound. In a post-training vocal assessment, eight of the nine individuals that were successfully trained to produce AG sounds generalized the use of these newly acquired signals to communicatively relevant situations. Chimpanzees possess the ability to acquire the use of a communicative signal via operant conditioning and can generalize the use of this newly acquired signal to appropriate communicative contexts.

Keywords

Chimpanzee; vocal learning; human language origins; speech

1. Introduction

Vocal learning and voluntary control over vocal production are key components of human spoken language. Although there is evidence of vocal learning in songbirds, and a few species of mammals, reports of vocal learning in non-human primates, including chimpanzees (*Pan troglodytes*), our closest phylogenetic relatives, are scarce (see Fedurek & Slocumbe, 2011; Seyfarth & Cheney, 2010 for recent reviews). Specifically, the majority of available data indicate that chimpanzees have very little voluntary control over which vocalization they produce in a given situation, and that the acoustic features of these vocalizations are largely innate and show little if any effect of learning (Foundas, Bollich, Corey, Hurley, & Heilman, 2001; Goodall, 1986; W. D. Hopkins, Taglialatela, & Leavens, 2011; Seyfarth & Cheney, 2010). However, there is some evidence that chimpanzees do

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have control over the initiation of some of their vocalizations and can suppress certain calls in response to changes in audience composition (Slocombe et al., 2010; Townsend, Deschner, & Zuberbühler, 2008). Notwithstanding, the general consensus regarding the vocal repertoires of nonhuman primates (including chimpanzees) is that they are genetically determined and largely fixed in both form and usage (Fedurek & Slocombe, 2011; Seyfarth & Cheney, 2010).

In the late 1940's and early 1950's, a chimpanzee named Vicki was raised in a human home in one of a few cross-fostering studies that attempted to examine the effect that human enculturation would have on a chimpanzee (Hayes & Hayes, 1951). Specifically, the researchers made deliberate attempts to teach Vicki to produce spoken English words. However, after six years of training, Vicki was only able to produce four hardly-intelligible words. The Hayes' concluded that Vicki did not possess the level of motor control needed for producing human-like speech. However, it is worth noting, that Vicki *did* learn to produce voiced sounds voluntarily indicating a previously unrecognized level of vocal control in chimpanzees. In a second early study, Randolph and Brooks (1967) successfully conditioned a single male juvenile chimpanzee to produce a "low guttural bark." Using social play as a reinforcer, the researchers showed that the juvenile chimpanzee learned to discriminate between 2 visual stimuli (a human experimenter standing in front of the subject's enclosure with her hand on the wire mesh and the experimenter standing in front of the subject's enclosure with her back to the subject), and produce the appropriate vocal response only in response to the second stimulus (i.e. back to the cage). Although there are considerable limitations regarding the conclusions that can be drawn from this early work, taken together, the results from these two studies seem to suggest that chimpanzees do have some voluntary control over their vocal production – at least in terms of the initiation of sound production.

In addition, there is evidence that chimpanzees can modify the structure of at least some of their calls (Crockford, Herbinger, Vigilant, & Boesch, 2004; Marshall, Wrangham, & Arcadi, 1999). For example, Marshall, Wrangham and Arcadi (1999) demonstrated that pant hoots of captive male chimpanzees living in two different facilities in the U.S. are acoustically distinct between groups although it was not possible to control for potential acoustic parameters of the different environments. They also reported that when a male chimpanzee was introduced into a new social group, he modified his pant hoots to match those of his new group. More recently, Crockford and colleagues (2004) reported structural differences in the pant hoot vocalizations of male chimpanzees living in neighboring communities, but not between groups from a distant community. These results could not be accounted for by genetic or habitat differences suggesting that the male chimpanzees may be actively modifying the structure of their calls to facilitate group identification (Crockford et al., 2004). These studies indicate that both in the wild and in captivity, male chimpanzees seem to be able to modify their pant hoots presumably so that their calls are similar to individuals in their community, but different from those produced by individuals in neighboring groups.

Despite this evidence that chimpanzees modify the acoustic structure of their pant hoot vocalizations (Crockford et al., 2004; Marshall et al., 1999) and alter the production of copulation and food calls based on the composition of their audience (Slocombe et al., 2010; Townsend et al., 2008), chimpanzee vocalizations are still regarded as relatively fixed in terms of the ability to learn new vocalizations as well as the ability to produce various calls flexibly in a single context (Seyfarth & Cheney, 2010; but see Snowdon, 2009; Zuberbühler, 2005). However, recent studies have shown that captive chimpanzees (and orangutans) produce idiosyncratic sounds with their lips, mouths, and/or larynx that are collectively referred to as 'attention-getting' (AG) sounds (Cartmill & Byrne, 2007; W. D. Hopkins,

Taglialatela, & Leavens, 2007). There is a growing body of evidence indicating that these sounds are used intentionally to capture the attention of an otherwise inattentive human (W. D. Hopkins et al., 2007; Hostetter, Russell, Freeman, & Hopkins, 2007; Liebal, Pika, Call, & Tomasello, 2004; Russell et al., 2005; Theall & Povinelli, 1999). Specifically, chimpanzees produce AG sounds more often when a human is present in conjunction with a desirable food item than when either is presented alone (W. D. Hopkins et al., 2007). In addition, chimpanzees are more likely to produce these sounds when a human is facing away from them (or has their eyes covered) than when the experimenter is looking at them (Hostetter et al., 2007; Leavens, Hostetter, Wesley, & Hopkins, 2004). It has also been demonstrated that AG sounds are not necessarily tied directly to food as chimpanzees are capable of utilizing AG sounds to request tools as well (Russell et al., 2005). It is important to note that AG sounds are not defined by a single acoustic structure, but are identified by the way in which they are used (W. D. Hopkins et al., 2007; Taglialatela, Reamer, Schapiro, & Hopkins, 2012).

Another factor that makes AG sounds interesting in the context of vocal learning is that not all captive chimpanzees produce these signals despite being raised and living in similar environments (W. D. Hopkins, Taglialatela, Leavens, Russell, & Schapiro, 2010; W. D. Hopkins et al., 2011; Taglialatela et al., 2012). Although it is not clear what factors account for the individual differences seen in the acquisition and use of this communicative signal, a recent study suggests that social learning might play an important role. Taglialatela and colleagues (2012) reported that AG sounds are socially learned via transmission from mothers to their offspring. Specifically, a significant association was found between mother and offspring AG sound production. Those chimpanzees who were raised by their biological mother were more likely to produce AG sounds (if their mother does), or not produce AG sounds (if their mother does not) than individuals that had been raised by humans in a nursery environment. However, rearing condition had no effect on whether or not an individual produces AG sounds. In other words, chimpanzees raised by their biological mothers were no more or less likely to produce AG sounds than those raised in a nursery environment, but mother-reared chimpanzees were more likely to be concordant with their mothers in the use of AG sounds than were the nursery-reared individuals. Therefore, we speculated that those chimpanzees raised in a nursery environment that *do* produce AG sounds might similarly have acquired the use of these signals through social learning, but perhaps from their peers just as other individuals had apparently learned them from their mothers.

We hypothesized that if social learning does play a role in the acquisition and use of these signals, we might be able to teach a chimpanzee to produce AG sounds using positive reinforcement. To this end, we first assessed a large population of captive chimpanzees (N=76) for their use of AG sounds. This vocal assessment consisted of six warm-up trials to establish that the subject was engaged with the experimenter and motivated to participate, followed by six test trials in which an experimenter approached the focal subject's home enclosure holding a cache of food, gained the subject's attention by calling his/her name and then stood at a 45 degree angle at the edge of the subject's enclosure facing the chimpanzees in the neighboring enclosure for a period of 60 seconds. All warm-up and test trials were followed by a 60 second inter-trial interval. The six test trials were audio/video recorded and subsequently coded for the presence or absence of AG sounds. Second, a subset of individuals that did not produce any AG sounds during the vocal assessment, but were known to be highly motivated to participate in training with humans were evaluated for their ability to acquire the use of an AG sound through operant conditioning and then to employ those sounds in an attention-getting context. Specifically, 14 chimpanzees were shaped using positive reinforcement to use their mouths to produce a sound. Common sounds included raspberries (a splutter sound produced when air is blown out through pursed lips)

and extended grunts (a voiced, grunt-like sound that is produced by vibration of the vocal folds). However, subjects were not required to produce sounds with a specific acoustic structure. For those individuals that did acquire this behavior ($n=9$), we repeated the vocal assessment to determine if they would generalize the use of this newly acquired signal to a communicative context to gain the attention of an otherwise inattentive human.

2. Results

2.1 Vocal Assessment

Subjects that produced at least one AG sound during at least one of the six trials were classified as AG+. Those individuals that never produced a single AG sound in any of the six trials were classified as AG-. Of the 76 chimpanzees tested on the vocal assessment, 44 did not produce an AG sound on any of the six trials and were classified as AG-. The remaining 32 subjects produced a minimum of one AG sound in at least one trial and were classified as AG+. Figure 1 depicts the number of individuals producing at least one AG sound in one, two, three, four, five and six trials respectively as well as the number of individuals that never produced an AG sound during the vocal assessment (represented in the "0 Trials" column). AG+ subjects included 12 males and 20 females whereas AG- subjects included 12 males and 32 females. A chi-square test revealed that the distribution of AG+ and AG- males and females did not differ significantly from chance, $X^2(1, N=76)=0.49, p=.48$. In addition, Taglialatela et al. (2012) reported that in their sample of 158 chimpanzees housed at the Michael E. Keeling Center for Comparative Medicine and Research in Bastrop, Texas, 85 did not produce attention-getting vocalizations and 73 did. A chi-square test revealed that the distribution of AG+ and AG- chimpanzees seen in our sample does not differ significantly from the distribution reported in the Bastrop colony, $X^2(1, N=234)=0.20, p=.65$.

2.2 Vocalization Training

Of the 14 subjects that participated in vocalization training, nine subjects successfully learned to produce AG sounds. Five subjects failed to show progress in ten consecutive training sessions and were considered unsuccessful. The nine successful subjects produced their first AG sound in one to ten training sessions (mean=6.33 sessions, median=7 sessions) or an average of 70.45 minutes of training. Furthermore, once each of these chimpanzees produced their first AG sound, they consistently produced AG sounds in all following sessions (with the exception of Abby who had one subsequent session without an AG sound). Once each subject produced their first AG sound, they reached criterion (defined as producing AG sounds in 10 training sessions) within 10 or 11 subsequent training sessions (see Figure 2) or an average of 139.80 minutes.

For the nine individuals (four males and five females) that were successfully trained to produce AG sounds, a post-training vocal assessment was administered to determine if the chimpanzees were generalizing the use of these newly acquired signals to communicatively relevant situations (i.e. when they needed to acquire the attention of an otherwise inattentive human social partner). The post-training vocal assessment followed the exact same procedures as the initial vocal assessment. Consistent with the initial vocal assessment, trials from the post-training test were coded by a second experimenter (JM) not involved in the vocalization training. Eight of the nine individuals that were successfully trained to produce attention-getting sounds did so in at least one trial during the post-training vocal assessment (see Figure 1).

Each individual learned to produce only one sound type during the training and continued to produce that sound type exclusively in the post training vocal assessment (with the

exception of Duff who did not produce an AG sound in his post training assessment). Five individuals produced extended grunts, two individuals produced raspberries, one individual made kisses and one produced an idiosyncratic AG sound that roughly sounds like a duck quacking (made by apparently passing air between the tongue and the back of the throat) that we classified as “other” (see Figure 3 for spectrograms of the four AG sound types acquired during vocal training). Thus, over half of the successful chimpanzees in our sample learned to produce the voiced, extended grunt, whereas the remaining subjects produced unvoiced sounds that were made by the filtering or resonance structures.

3. Discussion

The results presented here reveal that at least some chimpanzees are able to learn to produce an attention-getting sound through positive reinforcement training demonstrating a level of orofacial motor control previously thought to be absent in non-human primates. Furthermore, the nine successfully trained individuals acquired the behavior rapidly, producing their first AG sound in ten training sessions or less and, subsequently using the learned behavior in a communicative context to gain the attention of an otherwise inattentive human. These data are consistent with recent data suggesting that attention-getting sounds are used intentionally and are socially learned suggesting that this particular category of signal may stand apart from many other types of chimpanzee vocalizations (W. D. Hopkins et al., 2007; Taglialatela et al., 2012).

This study raises several questions. First, given the relative ease and speed with which the nine successfully trained individuals acquired this behavior, why did they never learn to produce AG sounds outside of the context of explicit training given their captive environment and daily interactions with humans? One possibility is that they have found other effective ways to accomplish the goal of gaining the attention of their human caregivers. A number of studies have described the variety of strategies (other than AG sounds) used by captive chimpanzees and other great apes to attract the attention of a human caregiver or experimenter including throwing, cage banging, clapping and spitting (W. D. Hopkins et al., 2007; Hostetter, Cantero, & Hopkins, 2001; Leavens et al., 2004; Leavens, Russell, & Hopkins, 2005; Poss, Kuhar, Stoinski, & Hopkins, 2006).

Second, it is possible that there are cognitive limitations in some chimpanzees that preclude them from being able to produce AG sounds. It is unknown as to whether or not the five unsuccessful subjects simply do not possess the motor or cognitive ability to learn this behavior or if they might acquire the ability with further training. We stopped training after 10 consecutive sessions without progress. It is possible that these subjects would have acquired the use of AG sounds with additional training or using different behavior modification strategies. Future research should focus on examining the behavioral, cognitive, genetic, and neurological differences between chimpanzees that utilize AG sounds and those that do not to determine in what other ways these individuals might differ.

In the current study, our sample of chimpanzees learned to use one of four different AG sound types (Figure 3) to acquire the attention of an inattentive human experimenter. Given that the sounds were not (prior to training) part of the chimpanzees' repertoire (as indicated by performance on the vocal assessment pre-test), the acquisition and use of the signal conforms to accepted definitions of production vocal learning (Janik & Slater, 1997, 2000; Petkov & Jarvis, 2012). In their 2000 review, Janik and Slater further divide production learning into respiratory system (changing sound parameters by altering the state of the respiratory muscles), phonatory system (changing sound parameters by altering the state of the sound-producing structures), and filter system (changing sound parameters by altering the state of filtering structures)

Utilizing these distinctions, the raspberry and kiss AG sounds can be described as production learning involving the filter system, whereas the extended grunt can be described as production learning involving the phonatory system.

Notwithstanding, some might argue that production learning is limited to voiced calls, thereby excluding some AG sounds. However, over half of our sample (N=5) of successfully trained chimpanzees learned to produce the voiced extended grunt (W. D. Hopkins et al., 2007; Taglialatela et al., 2012). Therefore, the findings reported here present the first experimental evidence of vocal production learning in chimpanzees. In addition, Janik and Slater (2000) noted that much of the information in human language is encoded by the filter system, and Petkov and Jarvis (2012) similarly point out that human speech is modified by labial and oro-facial control. Indeed, MacNeilage (2008) argued that the oscillations of mouth movements during lip smacking in monkeys is similar to the motor demands for phonemic production in human speech. Therefore, we propose that the acquisition and use of both voiced and unvoiced AG calls by the chimpanzees in our sample adds important information to our knowledge of pre-adaptations for speech that likely existed in our most recent common ancestor.

The results reported here demonstrate that chimpanzees not only possess the ability to acquire the use of a communicative signal via operant conditioning, but they are able to subsequently generalize the use of this newly acquired signal to appropriate communicative contexts. These data a) provide direct evidence supporting the hypothesis that chimpanzees have the capacity for vocal learning and b) suggest that chimpanzees have a previously unrecognized level of vocal control. Recently, Taglialatela and colleagues (2008, 2011) have reported that the chimpanzee homologue of the human Broca's area is selectively involved in the production of AG sounds – suggesting that this region that is critical for human language production and was already responsible for mediating the production of orofacial communicative signals prior to the split between the common ancestor of modern chimpanzees and humans. The potential effects that acquiring the use of this communicative signal may or may not have on the neurobiological structures and pathways that support the production of this signal are not clear. Notwithstanding, the acquisition and subsequent generalization and usage of this communicative signal suggest the potential for plasticity within this region. The vocal learning and flexibility seen in the chimpanzees in the current study along with the recent report that the chimpanzee Broca's area homologue is activated during the production of AG sounds (Taglialatela et al., 2008, 2011) suggests that the most recent common ancestor of humans and chimpanzees already possessed many important preadaptations that set the stage for the emergence of human speech.

4. Methods

4.1 Vocalization Assessment

4.1.1 Participants—Participants for the initial vocalization assessment included 76 chimpanzees (24 males, 52 females) ranging in age from 10 to 57 years, housed at the Yerkes National Primate Research Center, Atlanta, GA. All subjects were tested in their home enclosure. All chimpanzees voluntarily participated in testing and received a normal diet of fruit, vegetables, nuts, cereal, juice, water, primate chow, etc. during the study period.

4.1.2 Vocalization Assessment Procedure—Most YNPRC chimpanzees are trained to voluntarily separate from their social partners and are comfortable being alone for short periods of time. For the vocal assessment, most subjects are briefly separated from their social group (approximately 30 minutes) for testing. Those individuals not comfortable being alone are tested with one other social partner. Prior to testing, each subject received six, 60-second warm-up trials to ensure that they were engaged with the experimenter and

motivated to participate. In each warm-up trial, an experimenter sat down on a stool in front of the subject's enclosure and placed a small container of cut up fruit on the ground between themselves and the subject. The subject was given 60 seconds to respond after which, regardless of their communicative behavior, they were rewarded with a small piece of fruit.

The vocal assessment consisted of six, 30 second trials. Each trial was separated by a minimum 60 second inter-trial interval. At the beginning of each test trial, the experimenter approached the subject's home enclosure holding a container of food. The experimenter then acquired the subject's attention (i.e. made eye contact and spoke his/her name) and then stood at a 45 degree angle at the edge of the enclosure facing the focal chimpanzee's neighbors (i.e. chimpanzees living in the adjacent enclosure). Each trial was video recorded and later coded by a second experimenter (JM) for the presence or absence of at least one AG sound. Attention-getting vocalizations were defined as clearly audible sounds that are produced with the mouth, occur within the context of requesting food or attention from a human and are accompanied by overt visual monitoring of that human. Attention-getting vocalizations do not include food barks, food grunts, pant hoots, whimpers, screams, alarms or sounds made while actively grooming. Subjects that produce at least one AG sound during at least one of the six trials are classified as AG+. Those individuals that did not produce an AG sound in any of the six trials are classified as AG-.

4.2 Vocalization Training

4.2.1 Participants—Following the initial vocal assessment, chimpanzees were chosen for vocalization training based on two criteria. First, each chosen participant did not produce any attention-getting sounds on the vocal assessment designed to elicit this specific behavior [i.e. those that were classified as AG- as described above (n=44)]. Second, from these 44 subjects classified as AG-, we selected 14 individuals that were known to be highly motivated to interact with humans and to participate in positive reinforcement training for husbandry behaviors. These 14 chimpanzees (6 males, 8 females) participated in the vocal training procedures as described below. The subjects ranged in age from 15 to 32 years (mean=21 years).

4.2.2 Vocalization Training Procedures—Chimpanzees were trained to produce AG sounds using positive reinforcement techniques. Specifically, the trainer utilized “clicker training” in which a small, mechanical device that produces a clicking sound when depressed is paired with primary reinforcers to establish the “click” as a secondary reinforcer. Use of a secondary reinforce such as a “click” helps a trainer to more precisely mark the exact behavior being reinforced. Subjects participated in 0 to 4 training sessions per week with a maximum of two sessions a day (separated by at least 2.5 hours). Sessions occurred over a period of 1.03 to 3.03 months (mean training period = 1.55 months, median training period = 1.40 months). Sessions ranged in duration from 4.5 minutes to 22.25 minutes (mean session length = 10.45 minutes). Training sessions continued until either a) the subject produced an AG sound in 10 training sessions, considered successfully trained or until b) the subject showed no progress in 10 consecutive training sessions, considered unsuccessful.

The trainer utilized each chimpanzee's natural propensity to produce species-typical facial expressions and vocalizations in various contexts to capture behavior that was then shaped towards the end goal of AG sounds. It's important to note that we were much more interested in the outcome of vocal learning rather than the specific mechanisms through which the behavior might be acquired. Thus, while we did have a general shaping plan and consistently used only positive reinforcement through clicker training, we were flexible when it came to the exact procedures used during training.

In the basic vocal training shaping plan, initially any vocalizations or oro-facial gestures the subject produced were clicked and reinforced regardless of type or directionality. Examples of common behaviors reinforced during this step were lip pouts, open mouth gestures, food calls (barks and grunts) and pants. As the frequency of the reinforced behavior increased, only those signals that were directed towards the experimenter (indicated by eye contact) were reinforced. Furthermore, through using selective reinforcement, oro-facial gestures with audible exhalations of air, pursed or puckered lips and any attempts to intentionally vocalize were rewarded. As the subject progressed, he or she was selectively reinforced only for vocalizations that were increasingly louder and seemingly under voluntary control. Voluntary control was determined by the presence of several factors including eye contact, the production of the sound only when the trainer was present and the cessation of sound production once the subject heard the clicker and waited for his/her reinforcer to be delivered. In this way, subjects were taught to produce sounds with their mouths that met our definition of an AG sound.

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Highlights

- Chimpanzees can acquire the use of a communicative signal via operant conditioning
- Chimpanzees generalize the use of this signal to appropriate communicative contexts
- Chimpanzees possess the capacity for vocal learning

Figure 1.

Seventy six chimpanzees were assessed for their use of AG sounds to acquire the attention of an otherwise inattentive human social partner and could produce an AG sound in zero, one, two, three, four, five or all six of the six trials during this pre-training VA. In a post-training VA, the nine individuals that were successfully trained to produce an AG sound via positive reinforcement were evaluated for their ability to generalize the use of this signal in an appropriate communicative context and could produce an AG sound in zero to six of the six trials.

Figure 2.

The nine subjects that were successfully trained to produce an AG sound using operant conditioning produced their first AG sound in one to ten training sessions. We measured the number of additional training sessions following their first AG sound production needed to acquire reliable AG sound production, defined as producing AG sounds in ten training sessions. By adding the number of sessions until first AG sound production and the number of additional sessions required for reliable AG sound production, we calculated the total number of sessions needed to be successfully trained (“criterion”).

Figure 3.

Sound spectrograms of the four AG sound types acquired during vocalization training. A) Extended grunt: voiced, atonal sounds produced by the chimpanzees with an open mouth, B) Raspberry: produced by blowing air out through pursed lips, C) Kiss: produced by inhaling air through pursed lips, D) Other: vocalization that meets our definition of an AG sound but is not described by Taglialatela et al. (2012). In this case, the “other” is a quacking-type sound acquired by Lamar that seems to be made by passing air between the tongue and the back of the throat.