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Short Communication

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.

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 & Slocombe, 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; Hopkins, Taglialatela, & Leavens, 2011; Seyfarth & Cheney, 2010). However, there is some evidence that chimpanzees do 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, & Zuberbuhler, 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 1940s and early 1950s, 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,

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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, Herbinger, Vigilant, and Boesch (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; Zuberbuhler, 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; 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 (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 (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 (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 (Hopkins, Taglialatela, Leavens, Russell, & Schapiro, 2010; 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, Reamer, Schapiro, and Hopkins (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 s. All warm-up and test trials were followed by a 60 s 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+. Fig. 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