



Chimpanzees differentially produce novel vocalizations to capture the attention of a human

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Chimpanzees, *Pan troglodytes*, produce numerous species-atypical signals when raised in captivity. We examined contextual elements of the use of two of these vocal signals, the ‘raspberry’ and the extended grunt. Our results demonstrate that these vocalizations are not elicited by the presence of food, but instead function as attention-getting signals. These findings reveal a heretofore underappreciated category of animal signals: attention-getting sounds produced in novel environmental circumstances. The invention and use of species-atypical signals, considered in relation to group differences in signalling repertoires in apes in their natural habitats, may index a generative capacity in these hominoid species without obvious corollary in other primate species.

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A heretofore little-studied, yet theoretically important, class of animal signals are those produced uniquely within some populations but not within other populations of the same species. Nowak et al. (2000) listed three putatively exhaustive categories of animal communication designs: ‘a finite repertoire of calls...; a continuous analogue signal...; and a series of random variations on a theme’ (page 495). Clearly, the class of novel signals developed by animals is missing from that list. The number of such signals in both the auditory and visual domains is growing rapidly, with recent empirical research into the communicative repertoires of both captive and wild chimpanzees. Wild chimpanzees, *Pan troglodytes*, show a number of group differences in their communicative repertoires, including parametric, as opposed to qualitative, differences in their vocal repertoires (e.g. Crockford et al. 2004), and qualitative differences in their visual signals, including patchy distribution of the leaf-clipping display (Nishida 1980) and hand clasping while grooming (McGrew &

Tutin 1978). There are captivity-specific attention-directing manual gestures (e.g. pointing with fingers: Leavens et al. 2005a), other attention-getting auditory signals such as hand clapping (e.g. Hostetter et al. 2001; Leavens et al. 2004a) and facial expressions that serve as iconic gestures (e.g. Figure 1 in Leavens & Hopkins 1998). Far from being scientifically irrelevant consequences of artificial, captive environments, these signals are produced by chimpanzees who do not, presumably, differ systematically in their genetic complements from their wild counterparts (e.g. Leavens 2004; Leavens et al. 2005b). Common to all of these diverse signals is the complete absence of any overt attempt to train their development. Hence, chimpanzees generate novel signals in novel, artificial circumstances.

In contrast to the numerous studies on vocal communication in monkeys, very little research has focused on vocal communication in great apes. However, a few studies have reported that chimpanzees and bonobos, *Pan paniscus*, produce context-specific vocalizations in a number of ecological, social and behavioural situations (Crockford & Boesch 2003; Tagliatalata et al. 2003; Notman & Rendall 2005; Slocombe & Zuberbühler 2005). In addition, recent studies on captive chimpanzees have shown that they intentionally produce manual gestures (Call & Tomasello 1994; Tomasello et al. 1994;

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Krause & Fouts 1997; Hostetter et al. 2001; Leavens et al. 2004a). In these studies, food is typically placed outside the focal subject's home cage and is therefore out of reach from the subject. In these circumstances, chimpanzees and other great apes gesture to the food only when a human is present and visually oriented towards the subject (Call & Tomasello 1994; Tomasello et al. 1994; Leavens et al. 1996, 2004b; Krause & Fouts 1997; Hostetter et al. 2001; Poss et al. 2006). Moreover, chimpanzees alternate their gaze between the referent (food) and the social agent while gesturing (Leavens & Hopkins 1998) and 'repair' their gestural communication when it has failed (Leavens et al. 2005a).

Consistent with these findings, several studies have claimed that captive chimpanzees (and other apes) produce vocalizations and other nonvocal acoustic signals, such as banging their cage or hand clapping, as a means of capturing the attention of an otherwise inattentive social agent (Tomasello et al. 1994; Hostetter et al. 2001; Leavens et al. 2004a). Here we report characteristics of the use of two such signals, an extended grunt and a raspberry (this latter also known as a 'Bronx cheer' or 'splutter'). Both of these signals are common in captivity, but the raspberry has not, to our knowledge, been reported in any wild chimpanzee group (a similar sound has been reported in some, but not all, groups of wild orang-utans, *Pongo pygmaeus*, van Schaik et al. 2003). The raspberry is recognized by researchers to function as an attention-getting device (D. A. Leavens & W. D. Hopkins, unpublished data; R. W. Wrangham, personal communication), but has received very little experimental scrutiny (for a brief discussion of the raspberry see Marshall et al. 1999).

The primary aim of this study was to determine whether chimpanzees selectively produce 'raspberry' and 'extended grunt' vocalizations (herein referred to as attention-getting calls) to capture the attention of a human. To accomplish this goal, we compared the occurrence and frequency of attention-getting sounds and species-typical food vocalizations when either (1) a human alone was positioned in front of the chimpanzees, (2) food was placed in front of the chimpanzees with no human present and (3) food was placed in front of the chimpanzees and a human was standing in proximity to the food. Our hypothesis was that, if the attention-getting sounds are used to capture the attention of the human, then they should occur more frequently when a human and food are present together compared to either the human alone or food alone conditions. We further hypothesized that food calls would be produced more frequently when the food was presented alone compared to the human alone and human and food conditions.

METHODS

Subjects

Twenty-four subjects (15 females, nine males) ranging in age from 9 to 42 years old were included in this study ($\bar{X} \pm SD = 19.08 \pm 11.79$). All subjects were housed at the Yerkes National Primate Research Center (YNPRC) of

Emory University and had been used in previous studies on gestural and vocal communication (see Hostetter et al. 2001; Leavens et al. 2004a, 2005a). Our focus was to determine how chimpanzees use the raspberry and extended grunt (see Fig. 1), so we randomly selected the 24 subjects from a larger cohort of chimpanzees ($N = 55$) that had previously been identified to vocalize in the presence of a human holding food (see Leavens et al. 2004a).

Procedure

Subjects were tested in their home cages, either in isolation or in pairs. Each subject was tested once in three conditions: (1) food alone (FA); (2) human alone (HA); (3) human and food (HF). In the FA condition, an experimenter would place a whole banana on the ground outside the subject's home cage, 1 m from the subject, and would immediately leave the area. The human experimenter was familiar to all of the chimpanzees, and had worked with and frequently provided food to all subjects for 15 years. In the HA condition, the experimenter was positioned approximately 2 m in front of the subject. The human faced away from the focal subject and stood motionless for the duration of the trial (60 s). In the HF condition, the experimenter placed a banana 1 m from the subject and stood 2 m from the focal subject with their back to the focal subject. Each trial lasted 1 min and the order of presentation of the conditions was counterbalanced across subjects using the Latin Square technique (eight subjects tested in each of three different orders). In the FA and HF conditions, the food was hidden from the subject and therefore could not be seen until it was placed on the ground in front of the focal subject. All subjects were tested on the same day, with approximately 30 s between trials for each condition. All trials were videotaped with a digital video camera positioned on a tripod 1 m from the focal subject and scored later for the frequency of vocalizations in each condition. From the videotape, the experimenter recorded the number of attention-getting sounds and the number of food calls made by each subject in each condition during each 1-min trial. Occasionally the subjects pant-hooted during the trials but these were infrequent ($N = 4$) and therefore were not scored. Animals were not isolated from the rest of the colony during testing, because this practice would have introduced an element of artificiality into what was designed to be a fairly naturalistic procedure; that is, a situation in which the chimpanzees in their familiar social groups are faced with unreachable food, which is consistent with the life experiences of these subjects; social isolation is not a common experience for these animals and would, therefore, introduce an unnecessary confound into the procedure.

To assure reliability in measurement of the frequencies of occurrence of each vocal type, the videotapes were recoded 1 month after the initial data collection by the same observer who scored the original tapes. Tests from 10 randomly selected subjects were used to assess reliability. With respect to attention-getting calls, for the FA, HA and HF conditions, test-retest correlations were 1.0, 0.883 and

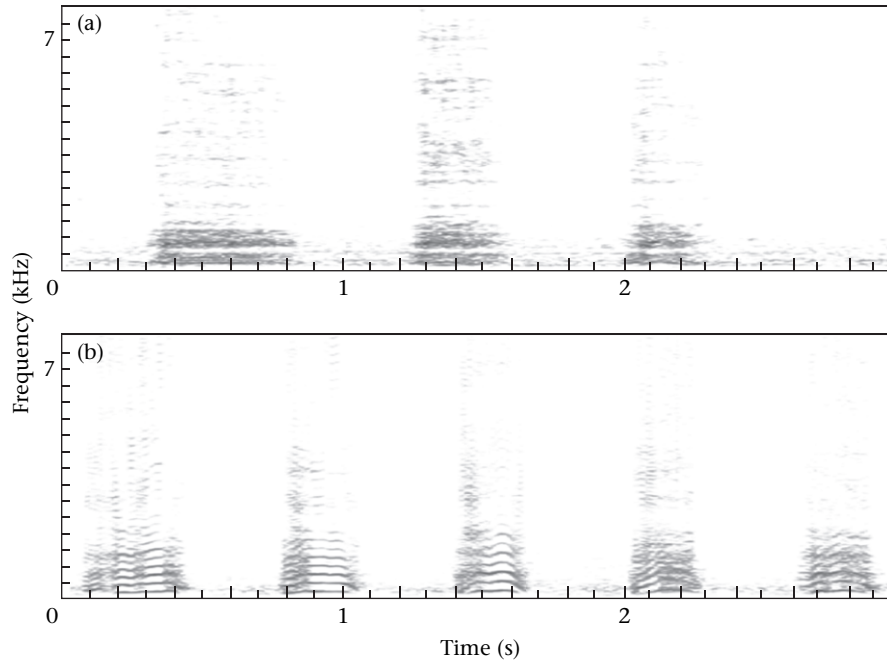


Figure 1. (a) Spectrograph of an ‘extended grunt’; (b) spectrograph of a ‘raspberry’ vocalization. Note that the apparent harmonic structure appears to be produced by labial vibrations rather than by vocal cord vibrations.

1.0, respectively. For the food calls, test–retest correlations for the FA, HA and HF conditions were 0.95, 1.0 and 1.0, respectively. Thus, intrarater agreements in recording the frequency of different vocal types were significant and high in each experimental condition. We also assessed inter-rater reliability. A second experimenter, who had neither previously scored nor seen any of the previous data or tapes, scored six of the individuals for the frequency of attention-getting calls and food calls in each of the three conditions. For the attention-getting sounds, test–retest correlations for the FA, HA and HF conditions were 1.0, 1.0 and 0.99, respectively. For the food calls, test–retest correlations for the FA, HA and HF conditions were 1.0, 1.0 and 0.90, respectively.

RESULTS

The total frequencies of each vocal type differed significantly between experimental conditions (Friedman test: attention-getting sounds: $\chi^2_2 = 21.81, P < 0.01$; food calls $\chi^2_2 = 13.77, P < 0.01$; Table 1). Subsequent post hoc tests indicated that the number of attention-getting sounds produced in the HF condition was significantly higher than in the HA (Wilcoxon matched-pairs signed-ranks test: $Z = 2.75, P < 0.05$) and FA ($Z = 3.63, P < 0.01$; Fig. 2) conditions. Similarly, post hoc tests indicated that the number of food calls produced in the FA condition was significantly higher than in the HA ($Z = 2.81, P < 0.01$) and HF ($Z = 2.09, P < 0.05$; Fig. 2) conditions.

In terms of individual variation in the vocal production between the three conditions, 71% of the chimpanzees produced at least one attention-getting call in the HF condition compared to only 29% in the HA condition and 8% in the FA condition. McNemar tests indicated that the

proportion of subjects producing an attention-getting sound in the HF condition was significantly higher than in the HA ($\chi^2_2 = 6.67, P < 0.02$) and FA ($\chi^2_2 = 14.06, P < 0.001$) conditions. There was no significant difference

Table 1. Individual data for each test condition and vocalization

Subject	Attention-getting calls			Food calls		
	HA	FA	HF	HA	FA	HF
Females						
Anja	0	1	15	0	0	0
Beleka	0	0	6	0	0	0
Brandy	2	0	4	0	58	3
Cathy	0	0	2	0	0	0
Cheeta	2	0	0	0	2	1
Dara	0	0	29	0	2	0
Edwina	2	0	6	0	0	0
Elvira	0	2	128	0	0	0
Faye	0	0	0	0	30	0
Leslie	0	0	0	0	0	0
Lilone	0	0	5	0	0	0
Liza	0	0	0	0	0	0
Mai	0	0	1	0	0	0
Melissa	0	0	10	0	0	0
Sylvia	3	0	3	0	0	0
Males						
Elwood	0	0	0	0	0	0
Fritz	1	0	6	0	2	6
lyk	0	0	1	0	0	0
Jarred	0	0	10	0	19	0
Jolson	0	0	4	0	38	43
Joseph	0	0	4	0	8	0
Les	0	0	0	0	8	0
Patrick	13	0	8	3	45	5
Winston	4	0	0	0	0	0

in the proportion of subjects producing attention-getting sounds in the FA and HA conditions. For the food calls, 42% of the chimpanzees made a food call in the FA condition compared to 21% in the HF condition and 4% in the HA condition. Similarly, McNemar tests indicated that the number of individuals producing food calls in the FA condition was significantly higher than that in the HA condition ($\chi^2_2 = 6.13$, $P < 0.01$). No other differences were significant.

In the next analysis, we compared the frequencies in the production of attention-getting calls and food calls across the three test conditions as a function of whether the chimpanzees were tested alone ($N = 9$) or with a cagemate ($N = 15$) (Table 2). This was done to assess whether the observed pattern of results might be due to the presence of an audience or emotional contagion. For each type of sound, we performed a mixed model ANOVA with condition (FA, HA, HF) as the repeated measure and housing condition (alone, with cagemate) as the between-group factor. For both food calls and attention-getting sounds, no significant main effects or interactions were found.

Lastly, to test whether the observed effects were specific to raspberries or extended grunts, we compared the frequencies of both vocalizations across conditions as a function of whether the chimpanzees made raspberries ($N = 17$) or extended grunts ($N = 7$) using a mixed model ANOVA. Test condition was the repeated measure and vocal type was the between-group factor. No significant main effects or interactions with the vocal type variable were found in these analyses.

DISCUSSION

In this study, we sought to determine whether chimpanzees selectively produce specific vocalizations to capture the attention of a human. We found that chimpanzees were more likely to produce two specific calls, the raspberry and the extended grunt (so-called 'attention-getting sounds'), when a human was present in conjunction with a preferred food item than when either stimulus (human, food) was presented alone. In addition, chimpanzees were more likely to produce traditionally defined 'food' vocalizations in the presence of food alone than they were when food was presented in conjunction with a human, or when a human was alone. These results suggest that chimpanzees use context-specific vocalizations and may intentionally produce these sounds.

These results indicate that captive chimpanzees alter the type of vocalizations that they produce depending on the

context and communicative demands of the situation. For example, when chimpanzees need to capture the attention of an otherwise inattentive human, they produce raspberry or extended grunt vocalizations and rarely produce food calls. In contrast, upon sight of food by itself, chimpanzees produce significantly more food calls compared to when a human is present alone or present in conjunction with the food. In other words, attention-getting sounds are used as a means of manipulating the attentional status of a human, whereas food calls appear to be associated with the presence of food. Reinforcing the view that the raspberry and extended grunt are used as attention-getting sounds is the evidence that they are also produced to capture the attention of a human facing away from them who is holding a tool needed for a problem-solving task (Russell et al. 2005). Thus, the presence of food in conjunction with a human is not the only condition under which raspberries and extended grunts are produced. Collectively, these results suggest that the chimpanzees produced these sounds intentionally. Interestingly, none of our subjects produced both the raspberry and the extended grunt. One possible explanation for this observation is that individuals that have acquired one of these two so-called attention-getting sounds do not need to produce a second type in order to achieve the intended result (i.e. producing a raspberry may be just as effective as producing an extended grunt at acquiring the attention of a human experimenter, so the chimpanzees may need only to incorporate one of these sounds into their repertoire). Certainly, this would speak to the functional equivalence of the two sounds. However, we have observed other chimpanzees at our facility (YNPRC) producing both the raspberry and extended grunt, and we plan to study the use of these two vocalizations more closely in the future.

Our results differ from those of previous studies that have documented audience effects in chimpanzees and other primates. In previous studies on chimpanzees, the rates of production of specific vocalizations were altered by parameters associated with either food quantity or divisibility (Hauser et al. 1993) as well as the absence or presence of a social partner (Brosnan & de Waal 2003). In contrast, in our study, rather than altering the rate at which specific vocalizations were produced in response to the presence or absence of an audience, chimpanzees produced different vocalizations depending on the presence or absence of a human in association with a food item. This suggests a functional distinction in the chimpanzees' use of vocalizations based on the communicative context. Although it is not clear whether the chimpanzees silenced their food vocalizations in the HF condition in favour of attention-getting calls, our results clearly indicate that the chimpanzees are controlling what sounds they produce. Moreover, the fact that the raspberry is not part of the species-typical repertoire of sounds in chimpanzees further supports the view that this sound has been individually learned by the animals, and that its production may involve a volitional component. Of course it remains possible that these sounds do exist in wild populations but have not yet been observed.

Table 2. Mean number of attention-getting calls and food calls given by chimpanzees as a function of housing condition

	Attention-getting calls			Food calls		
	HA	FA	HF	HA	FA	HF
Housing condition						
Alone	0.67	0.01	6.44	0.01	15.00	5.22
With cagemate	1.40	0.20	4.13	0.20	5.13	0.73

It is also possible that these putative attention-getting vocalizations were elicited by the presence of a human (as opposed to the apparent attentional status of the human), irrespective of the other factors that we manipulated, but we believe this is unlikely for two reasons. First, few such signals were displayed in the HA condition (see Fig. 2); it was, thus, the combined presentation of humans and food that elicited the majority of these particular vocalizations. In fact, the occurrence of attention-getting sounds in the HA condition were entirely attributable to being preceded by an HF trial in the three-trial sequence. Thus, there were some carryover effects from the HF to the HA condition because a human had previously been present with a food. Second, we know from previous research that chimpanzees are sensitive to the apparent attentional status of a communicative partner when communicative partners are conspecifics (Tomasello et al. 1994) and when the communicative partners are humans (e.g. Hostetter et al. 2001; Leavens et al. 2004a).

In our view, the best framework for the proximate interpretation of the current findings as well as previous results on gestural communication in captive chimpanzees is that apes engage in a form of social tool use in response to what has been referred to as the 'referential problem space' (Leavens et al. 2005b). Tool use has been defined as 'the external employment of an unattached environmental object to alter more efficiently the form, position, or condition of another object, another organism, or the user itself when the user holds or carries the tool during or just prior to use and is responsible for the proper and effective orientation of the tool' (Beck 1980, page 16). Wild and captive chimpanzees are well known for their tool-using abilities, and the results of our studies meet this definition. Within this framework, the chimpanzees have a goal, to obtain a food item that they cannot otherwise attain. In this context, the chimpanzees use their communicative behaviours to manipulate a human (the tool) to attain

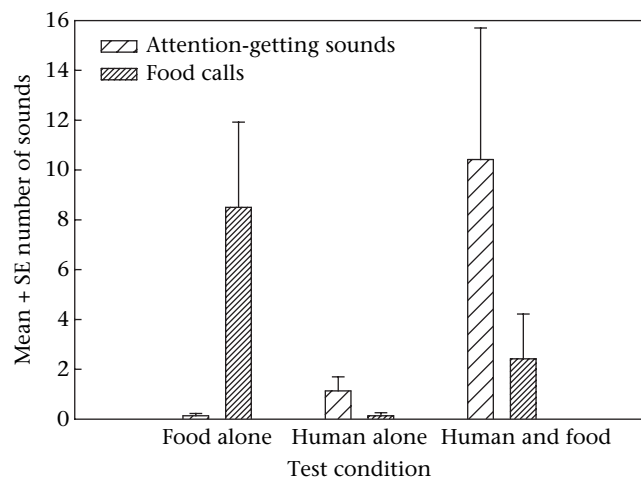


Figure 2. Mean + SE number of food calls and attention-getting sounds as a function of whether food was presented alone, a human was present alone or a human and food were presented at the same time.

a food item (goal). Moreover, their communicative behaviour is flexible in this context because the chimpanzees alter the modality of their communicative signals in accordance with the attentional state of the human. Specifically, when a human is facing them, they are more likely to use visual signals such as manual gestures, but when a human is facing away from them, they are more likely to use auditory signals, including vocalizations (Hostetter et al. 2001; Leavens et al. 2004a). Thus, both chimpanzees and humans can tactically deploy their communicative signals towards immediate ends, presumably using homologous problem-solving capacities (e.g. Leavens et al. 2005a, b).

The ultimate significance of these findings is that attention-getting vocalizations represent evidence for the invention and use of novel signals in a nonhuman animal, in instrumental contexts. The generative nature of chimpanzee communication has significance for our understanding of language evolution. This generative quality is frequently listed as a trait uniquely characteristic of human languages (e.g. Hauser et al. 2004), a claim that we believe is refuted by the diverse array of signals developed and used by chimpanzees to communicate with their human social partners. This creative potential displayed by chimpanzees evokes a mode of communication that may have relatively limited distribution among vertebrates. This mode is characterized by a persistent thrusting and parrying of signals, indicative of a strong motivation to cocreate meaning, what Tomasello & Call (1997) refer to as 'ontogenetic ritualization'. Whereas ontogenetic ritualization strictly denotes a process of signal acquisition, we suggest that there might be considerable variability across primate species in their motivation to engage in this process (e.g. Bard 1998). Clearly, other primates can discriminate and adaptively use ecologically relevant signals (e.g. Zuberbühler 2000), but what may distinguish the great apes from other anthropoids is the motivation for this creative or generative signal development. Chimpanzee signals lack the recursive qualities that truly set human languages apart (cf. Hauser et al. 2004), nevertheless, as far as we know, few other primates invent as wide a range of signals in such diverse modalities as do chimpanzees (cf. Tomasello et al. 1985, 1994), although this claim must be considered tentative in the absence of extensive comparative research into population-specific communicative signals. This multimodal generative capacity is implicit in several recent models of language evolution (e.g. Nowak et al. 2000; Hauser et al. 2004) and becomes especially evident when chimpanzees are raised in captive environments. Thus, the capacity not merely to discriminate but to generate novel communicative signals, which is a hallmark of human linguistic communication, may have relatively ancient roots in the signalling characteristics of our ape ancestors.

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