



# Playbacks of food-associated calls attract chimpanzees towards known food patches in a captive setting

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## Abstract

Food-associated calls have received much research attention due to their potential to refer to discovered food in a word-like manner. Studies have found that in many species, food-associated calls attract receivers to the food patch, suggesting these calls play roles in food sharing, cooperation and competition. Additionally, in various species, these calls play a role that has received much less attention: mediating social interactions among foragers that are already nearby or within the food patch, independently of whether they attract outside foragers. In order to increase understanding of the function of the chimpanzee (*Pan troglodytes*) food-associated rough grunt, we conducted captive playback studies testing whether rough grunt playbacks attract, repel or have no effect on the proximity of foragers already familiarized with the presence of food. We tested how acoustic playbacks of rough grunts (or control calls) from one of two known, identical feeding sites affected receivers' approach and feeding behaviors. More often than expected, participants first approached the feeding site from which rough grunts, but not control calls, were broadcast. However, neither condition increased the likelihood that participants fed first from a given site. Our results support the hypothesis that rough grunts elicit an approach response in receivers, while providing no evidence that they repel. In addition, our study provides evidence that receivers may approach rough grunts even if they do not intend to feed. We discuss the information rough grunts may convey to receivers beyond information about discovered food and the potential benefits signalers may gain from this calling behavior.

**Keywords** Food-associated call · Vocalization playback study · Rough grunt · Chimpanzee

## Introduction

Many species of birds and mammals produce vocalizations while foraging (Clay et al. 2012). These 'food-associated calls' have attracted substantial research attention since patterns of call production may be capable of providing

information about the presence, quality, preference level, abundance or even identity of discovered food (Benz et al. 1992; Caine et al. 1995; Chapman and Lefebvre 1990; Di Bitetti 2005; Elowson et al. 1991; Hauser and Wrangham 1987; Marler et al. 1986; Slocombe and Zuberbühler 2005). These information-sharing properties have led some researchers to label food-associated calls as 'functionally referential signals' (Evans and Evans 1999; Kitzmann and Caine 2009; Slocombe and Zuberbühler 2005) and look toward this calling behavior for insights into the evolutionary origins of human language (Fedurek and Slocombe 2011; Zuberbühler 2003). Nevertheless, food-associated calls represent an evolutionary puzzle since drawing attention to discovered food may attract other foragers to the feeding site (Brown et al. 1991; Chapman and Lefebvre 1990; Elgar 1986a; Heinrich 1988; Laidre 2006). Such behavior has the potential to reduce the signaler's food intake (Di Bitetti and Janson 2001; Hake and Ekman 1988; Laidre 2006) and thereby negatively affect the signaler's reproductive success. Despite substantial research interest in food-associated

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calling behavior, how signalers benefit from producing these signals remains unclear for many species (Clay et al. 2012). Since signals are only expected to evolve when signalers gain a net benefit from the change in behavior elicited from receivers (Krebs and Dawkins 1984), identifying the effects food-associated calls have on receiver behavior is key to understanding the evolutionary origins of this seemingly altruistic communication behavior.

Most research exploring the function of food-associated calling behavior has focused on its ability to inform others of discovered food and/or attract them to the food source. Studies indicate that the food-associated calls of some species can promote food-seeking behavior in receivers (Evans and Evans 1999 2007), increase the likelihood that others approach the discovered food (Chapman and Lefebvre 1990; Elgar 1986a; Heinrich 1988), reduce the amount of time it takes for others to arrive at the food patch (Chapman and Lefebvre 1990; Elgar 1986a), or increase the total number of individuals that arrive (Brown et al. 1991; Laidre 2006). Signalers may benefit from this increase in foraging group size through a reduction in predation risk or vigilance levels (Chapman and Lefebvre 1990; Elgar 1986b), an increase in mating opportunities (Evans and Marler 1994) or an increase in the signaler's ability to defend the discovered food (Heinrich 1988). These studies support the assumption that food-associated calls attract others to the food patch and suggest that, despite a potential increase in feeding competition, some species gain a net benefit by increasing foraging group size or neighbor proximity.

While many food-associated vocalizations have been found to attract others to the food source, for some species, such attraction may be unrelated to the function of food-associated calling behavior from the signaler's perspective or may be only one of many ultimate functions of call production (Boinski and Campbell 1996; Gros-Louis 2004a; Heinrich and Marzluff 1991; Janik 2000). For example, the food-associated calls of vagrant ravens (*Corvus corax*) have been found to attract other vagrants towards the food patch, increasing the signaler's ability to collectively defend the food source from territory holders (Heinrich 1988). However, there is also evidence that the proximate causes of food-associated call production in vagrant ravens is hunger and high status and that such calling behavior may facilitate the establishment and/or maintenance of the signaler's dominance status during social interactions that take place at the food patch (Heinrich and Marzluff 1991). As another example, while playbacks of the food-associated calls of white-faced capuchins have been found to attract receivers who are unaware of the food patch (Gros-Louis 2004b), their food-associated calling behavior under natural conditions has been found to correlate with an increase in spacing between individuals already foraging within the patch (Boinski and Campbell 1996) and a reduction in the

likelihood that the signaler is closely approached, or receives aggression, by other foragers (Gros-Louis 2004a). Lastly, not all food-associated calls have been found to attract others. For example, Radford and Ridley (2008) found that the food-associated calls of pied babblers (*Turdoides bicolor*) do not attract others toward the signaler, but rather reduce the likelihood that others approach the signaler while foraging. Thus, many food-associated calls appear to mediate social interactions among foragers, independently of whether they attract outside individuals towards discovered food. Animal vocalizations are considered to fall on a continuum between containing only motivational information and only referential information, with most vocalizations falling somewhere in between (Marler et al. 1992). Thus, the strong research focus on the referentiality of food-associated calling behavior has the potential to hinder a more comprehensive understanding of the effects food-associated calls have on receivers (Owren and Rendall 2001).

Recently, many studies have focused on the food-associated 'rough grunt' of chimpanzees (*Pan troglodytes*). The term 'rough grunt' encompasses a set of graded signals that range from noisy, low-pitched grunts to tonal, high-pitched barks (Marler and Tenaza 1977; Slocombe and Zuberbühler 2006), and calling bouts can vary from one to many vocalizations (Brosnan and de Waal 2000; Fedurek and Slocombe 2013). In contrast to the chimpanzee 'pant hoot' vocalization, which may be produced upon arrival at a food patch and in a variety of other contexts (Clark and Wrangham 1994), rough grunts are only produced in foraging contexts (Goodall 1986). Because of the rough grunt's contextual specificity, it has been labeled a functionally referential signal (Slocombe and Zuberbühler 2005), and several studies have explored its ability to provide others with information about discovered food. These studies suggest that the production and acoustic properties of rough grunts may vary based on the quality (Fedurek and Slocombe 2013; Slocombe and Zuberbühler 2006), divisibility (Brosnan and de Waal 2000; Hauser et al. 1993) or identity of some foods (Slocombe and Zuberbühler 2005), and receivers can use this information to guide their foraging efforts (Slocombe and Zuberbühler 2005). Furthermore, there is evidence that rough grunts attract receivers towards food patches in some contexts (Kalan et al. 2015; Kalan and Boesch 2015). Accordingly, researchers have proposed that rough grunts play an important role in chimpanzee societies by facilitating the sharing of food with group members in return for social benefits (Brosnan and de Waal 2000; Kalan and Boesch 2015; Slocombe et al. 2010).

Despite some evidence that rough grunts attract others towards a food patch, studies indicate that rough grunts are typically produced when many receivers are already nearby, or inside, the food patch and are likely already aware of the presence and properties of the food (Fedurek and Slocombe

2013; Ischer et al. 2020). Even more, field studies have largely failed to replicate captive findings indicating that rough grunts convey detailed information about discovered food (Kalan et al. 2015; Slocombe and Zuberbühler 2006) (though see (Fedurek and Slocombe 2013)). Rather, social context has been found to play a central role in rough grunt production (Brosnan and de Waal 2000; Fedurek and Slocombe 2013; Ischer et al. 2020; Kalan and Boesch 2015; Schel et al. 2013; Slocombe et al. 2010). For example, a study by Fedurek and Slocombe (2013) found that chimpanzees produce rough grunts when they, themselves, are motivated to forage in a given food patch and that rough grunt production was correlated with an increased likelihood that close associates remained in the vicinity while the signaler fed. Another study found that rough grunt production was positively associated with the occurrence of aggressive events during feeding bouts and their production was more likely to occur after an aggressive event had taken place rather than before (Ischer et al. 2020). Thus, there is high potential that rough grunts provide socially relevant information to nearby foragers, rather than, or in addition to, information about food. More studies are needed to examine the effect rough grunts have on receiver behavior above and beyond any contextual information they may convey about a potential foraging opportunity.

To increase understanding of the function of the rough grunt vocalization, we designed a captive playback experiment that tests the effect rough grunt playbacks have on receiver proximity in a foraging context. In our study, participants had the opportunity to approach either a silent feeding site or one from which the rough grunts of a familiar group member had been broadcast. Using this experimental setup, we tested whether rough grunts attract, repel or have no effect on receiver proximity and foraging behavior when broadcast from known feeding sites. Since rough grunts are widely assumed to be affiliative food-sharing signals, experimentally testing whether receivers are attracted towards a feeding site from which rough grunts have been broadcast would strengthen support for this hypothesis. We predicted that, if rough grunts attract others towards the signaler, participants would first approach the feeding site from which rough grunts were broadcast. By providing participants with the silent feeding site, we aimed to reduce the likelihood that participants would approach the stimulus simply because it was their only option for acquiring food. While testing whether rough grunts attract others, we simultaneously tested whether they repel. Studies indicate that adult males produce rough grunts more often when in the presence of many males (Kalan and Boesch 2015) and when a more dominant male is in the vicinity (Schel et al. 2013), and rough grunts are also produced more often following the occurrence of aggressive events during feeding bouts (Ischer et al. 2020). While there is no evidence that rough grunts are

agonistic signals [e.g., they are also produced in the presence of close social partners (Slocombe et al. 2010) and sexually receptive females (Kalan and Boesch 2015)], they have the potential to function similarly to the vocalizations of white-faced capuchins (Gros-Louis 2004a) by claiming a feeding site and/or increasing spacing between foragers (Kalan et al. 2015). These behaviors could help facilitate co-feeding and/or reduce the likelihood of aggression when many individuals are feeding together in the same patch (Radford and Ridley 2008). If rough grunts locally repel others, we predicted that participants would first approach the silent feeding site. If rough grunts neither attract nor repel, or if rough grunts elicit a response in receivers solely by providing information about the presence of food, we predicted that participants would be equally likely to approach either feeding site since they were already aware of the presence and identical quality of the two food sources. For example, a study of food-associated calling behavior in chickens (*Gallus gallus*) found that while chickens responded with food-seeking behavior when broadcast playbacks of food-associated calls, this effect was eliminated when receivers had already discovered food themselves (Evans and Evans 2007).

In our study, each of 12 participants were presented with one Rough Grunt condition as well as a Control Call condition and a Silence condition. During the Control Call condition, we broadcast species-specific vocalizations other than rough grunts (pant hoot, pant grunt or raspberry) while keeping the identity of the signaler consistent within participants across the two stimulus conditions. The Control Call condition enabled us to test whether receiver responses in the Rough Grunt condition could be explained simply as a response to the perceived presence of a familiar group member. The Silence Condition was designed to test whether there was a significant side bias across participants in the absence of stimuli which aided interpretation of participant responses in the Rough Grunt and Control Call conditions.

## Material and methods

### Study site and participants

All procedures performed in these studies adhered to the ethical standards in the protocols approved by the IACUCs of The University of Texas MD Anderson Cancer Center (UTMDACC) and the University of Minnesota (Protocol number # 1002A78194). L.O'B. ('the observer') collected data from chimpanzees housed at the National Center for Chimpanzee Care (NCCC) at the Michale E. Keeling Center for Comparative Medicine and Research of UTMDACC in Bastrop, TX. This site houses a large population of chimpanzees that reside in approximately 20 multi-male, multi-female social groups. As part of their normal living

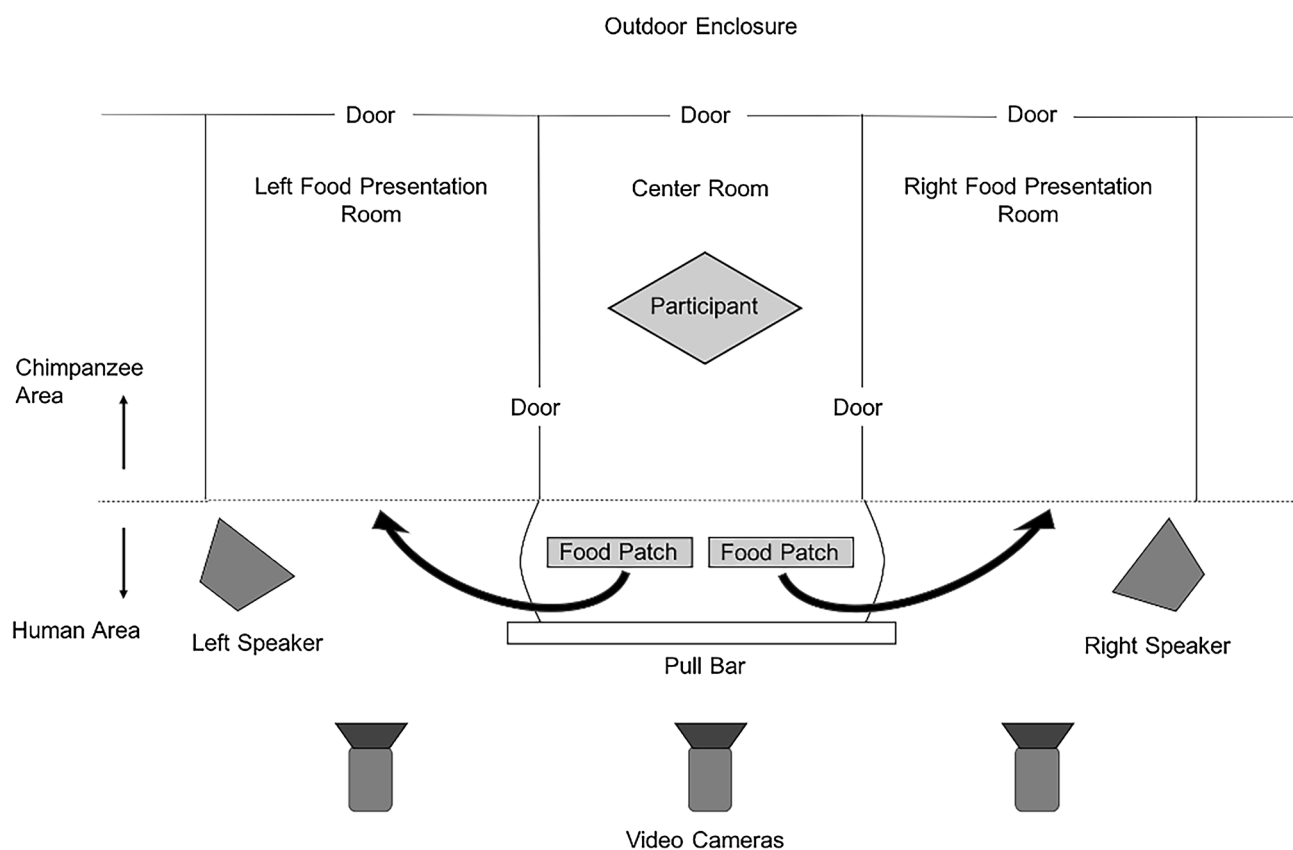
conditions, all animals involved in the study had ad libitum access to an indoor and outdoor enclosure, as well as to monkey chow and water. In addition, individuals were fed four fresh produce meals per day and participated in food-and/or drink-related enrichment activities multiple times each week. 12 adult chimpanzees (7 female and 5 male, Supplemental Table 1) from two different social groups *voluntarily* participated in our study. These participants were not deprived of food or water at any time during the study and had access to chow and water during all trials. While participants did occasionally drink water during trials, none consumed chow.

## Setup

The study environment consisted of each social group's three adjacent indoor rooms positioned in a row (Fig. 1). Each room had a sliding door separating it and its adjacent room(s), as well as the outdoor area. All doors could be manipulated by the observer from outside of the chimpanzee area (the 'human area'). The walls separating the chimpanzee and human areas were largely made of wire

mesh, enabling the observation and documentation of the participants' behavior from the human area. One video camera on a tripod was positioned in the human area outside of each of the three rooms, focusing on the center of each room. This enabled the participant's activity to be documented as it traveled in and between each room. The walls between each of the three rooms were opaque so that participants could not see the insides of each room without looking through an open door or entering the room.

Each feeding site consisted of 60 grapes resting in a trough composed of a polyvinyl chloride (PVC) pipe that had been cut in half lengthwise. We chose grapes as the food item in this study because food choice tests conducted by Hopper et al. (2013) indicate that they are a preferred food in this population of chimpanzees. Similar to other enrichment devices used to engage chimpanzees at this study location, as well as devices used in previous studies (O'Bryan et al. 2020), we attached the food to the outside (i.e., human side) of the wire mesh between the human and chimpanzee areas so that they could be readily attached and detached by the observer. Participants consumed the



**Fig. 1** The setup as it looked just after the participant voluntarily entered the study area from the outdoor enclosure. Note that the figure is not drawn to scale. The arrows indicate where the observer

placed the food patches prior to the initiation of playback. The pull bar was used to simultaneously open both doors between the center room and food presentation rooms, allowing the participant to enter

grapes by sticking their fingers through the mesh and pulling the grapes through the openings.

We broadcast vocalizations to participants through one of two speakers (Mackie SRM 350v2) placed in the human area just outside of each side room and angled toward the center room (Fig. 1). The center of each speaker was positioned approximately at the height of each feeding site. The speakers could not be seen by the participants from the center room, but could be viewed once the participant entered the food presentation rooms. Since we never broadcast vocalizations when the participant was in view of the speakers, and since the speakers were within view even during trials when no vocalizations were broadcast, we did not expect participants to associate these speakers with the vocalization playbacks. A laptop containing the stimulus sound files was placed in the far corner of the human area.

## Procedure

All participants experienced two training trials and three study trials and participants engaged in no more than one trial per day. The training trials were carried out in a similar manner as the study trials except that no stimuli of any kind were presented to the participants. At the start of each trial, all doors in the study area were in the closed position. Participants voluntarily entered the study area when the door between the outdoor enclosure and the center room was opened. This door remained open for the entirety of each participant's first training trial, enabling the participant to gradually explore the study area while also having access to the outdoor enclosure. During subsequent trials, the observer closed the door behind the participant once it entered the center room. If a participant did not appear entirely comfortable at any time during the study, the observer could open the door to the outdoor enclosure so that the participant could choose to go back outside. However, no participants displayed discomfort during any study trials or had to be returned to the outdoor enclosure prematurely.

At the time of the participant's entry into the center room, the two food troughs were lying next to one another on the ground in the human area just outside of the center room, so that the participant could observe the presence and equal quality of both food sources (Fig. 1). Once the participant was inside the center room and the outside door was closed, the observer attached one food trough to the wire mesh of one of the food presentation rooms. The observer then attached the other trough to the other room in the same manner. We randomly selected the side to which a trough was first attached before each trial. During the study trials, the observer initiated the playback once the food was placed.

Each trial represented one of three treatment levels: 'Silence', 'Rough Grunt' and 'Control Call.' Each participant experienced all three treatment levels in a randomized

order. For a given participant, the identity of the individual producing the rough grunt and control call was kept consistent (Table 1). During both the Rough Grunt and Control Call conditions, a rough grunt or control call, respectively, was broadcast from one of the two speakers while a silent stimulus was broadcast from the other. We randomly selected the side from which the rough grunt or control call was broadcast before each trial. The observer initiated the playback by discretely pressing play on a remote control while standing in the human area in line with the middle of the center room. Once the playback was completed, the observer simultaneously opened the sliding doors separating the center room from the two food presentation rooms using a pull bar that was connected to each of the two doors (Fig. 1). Once the doors were opened, participants were capable of freely entering both rooms. Once all of the food was consumed from both rooms, the observer opened a door to the outdoor enclosure so that the participant could exit the study area. The Silence condition was carried out in the same manner as the Rough Grunt and Control Call conditions, except that an empty stimulus file was broadcast from both speakers.

## Playback stimuli

L.O'B. recorded all playback stimuli with a Sennheiser ME66 shotgun microphone with K6 power module and a Marantz PMD670 recorder. Recorded rough grunts represented a range of acoustic variants (Fig. 2). Most rough grunts were recorded ad libitum during regular mealtimes and/or social interactions within the group. However, some rough grunts were elicited by placing food (grapes or other produce) inside the chimpanzees' enclosures. While results of some studies suggest that the acoustic properties of rough grunts may be capable of conveying information about food quality or even food type (Brosnan and de Waal 2000;

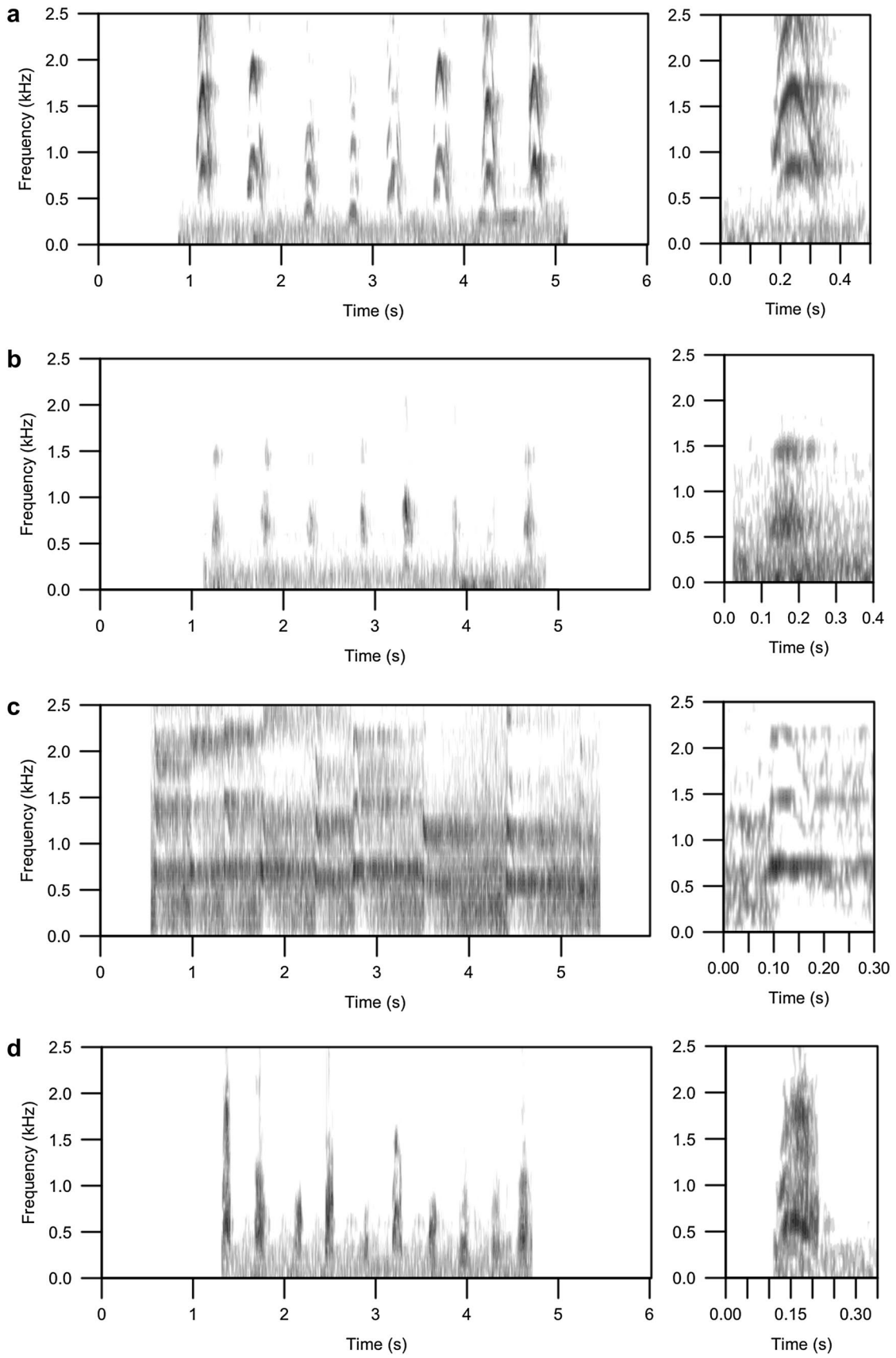
**Table 1** Playback stimulus information

Stimulus pair ID <sup>a</sup>	Group ID <sup>b</sup>	Signaler ID <sup>c</sup>	Participant ID	Control call type
A	1	JD	BD, PT, KB	Raspberry
B	1	BD	JD, TK, QY	Pant grunt
C	2	KP	BK, GI, NO	Pant grunt
D	2	RE	KK, KP, TA	Pant hoot

<sup>a</sup>Stimulus Pair ID represents a unique stimulus pair and corresponds with the stimuli presented in Figs. 2 and 3 and Supplemental Fig. 2

<sup>b</sup>Group ID represents the social group in which both the signaler and participant resided

<sup>c</sup>The signaler's vocalizations were used to create the playback stimuli for each participant listed in the Participant ID column. For each participant, the identity of the signaler was held consistent for both the Rough Grunt and Control Call conditions



**Fig. 2** Spectrograms of the rough grunt vocalizations used as stimuli in the Rough Grunt condition. Letters a through d correspond to the Stimulus Pair ID listed in Table 1. Darker shades of grey represent louder relative amplitudes. The panels on the left display the full stimuli used for playback and the panels on the right show a close up of one vocalization from each stimulus. Spectrograms were generated using the spectro function in *R* (version 4.0.5) with a window length of 512, an amplitude range of 40 dB at 5 dB intervals and overlap of 50% between successive analysis windows

Fedurek and Slocombe 2013; Hauser et al. 1993; Kalan et al. 2015; Slocombe and Zuberbühler 2005, 2006), other results do not support this hypothesis (Kalan et al. 2015; Slocombe and Zuberbühler 2006). Here we focus on the question of whether rough grunts are generally attractive or repulsive. Therefore, we do not expect the specific stimulus that elicited the calls to affect behavior at this level. Stimuli were recorded from four different individuals, two from each social group. One rough grunt and one control call stimulus was created from the recordings obtained from each of the four signalers (Table 1). There is no ideal control call since all vocalizations are thought to have evolved to impact the behavior of receivers in some way, and receivers are capable of flexibly extracting information from the vocalizations they perceive (Krebs and Dawkins 1984; Seyfarth and Cheney 2010). Thus, we designed our Control Call condition to simulate the presence of a familiar chimpanzee that is producing vocalizations with a similar call structure to rough grunts. Within study participants, the identity of the signaler was kept consistent across the Rough Grunt and Control Call conditions so that the only difference between conditions was the call type presented. Two of the control calls used in the study were ‘pant grunts’: grunts produced in rapid succession towards higher ranking chimpanzees (Bygott 1979; Goodall 1986). One of the control calls consisted of the quieter first phases of a ‘pant hoot’: a long-distance call produced in a variety of contexts, including foraging contexts (Reynolds and Reynolds 1965; Wrangham 1977). The truncated pant hoot we selected was comprised of only the introduction and build-up phases, which consist of a series of short call elements, and did not include the louder and more distinctive climax phase or the let-down phase (Arcadi 1996). Such a call is not unusual since wild chimpanzees also sometimes give truncated pant hoots with just these first phases (N. Desai, unpublished data). The other control call was a ‘raspberry’: labial vibrations frequently produced in captive environments to catch the attention of humans, particularly in the presence of food (Hopkins et al. 2007). We reduced the stimulus length to a duration of 6 s (if needed) but otherwise did not edit the stimuli. We cropped the stimulus files using Praat Version 5.1.34 ([www.praat.org](http://www.praat.org)) and broadcast the signals using Windows Media Player (Version 11). Figures 2 and 3 display spectrograms of the stimuli presented in the Rough Grunt and Control Call conditions,

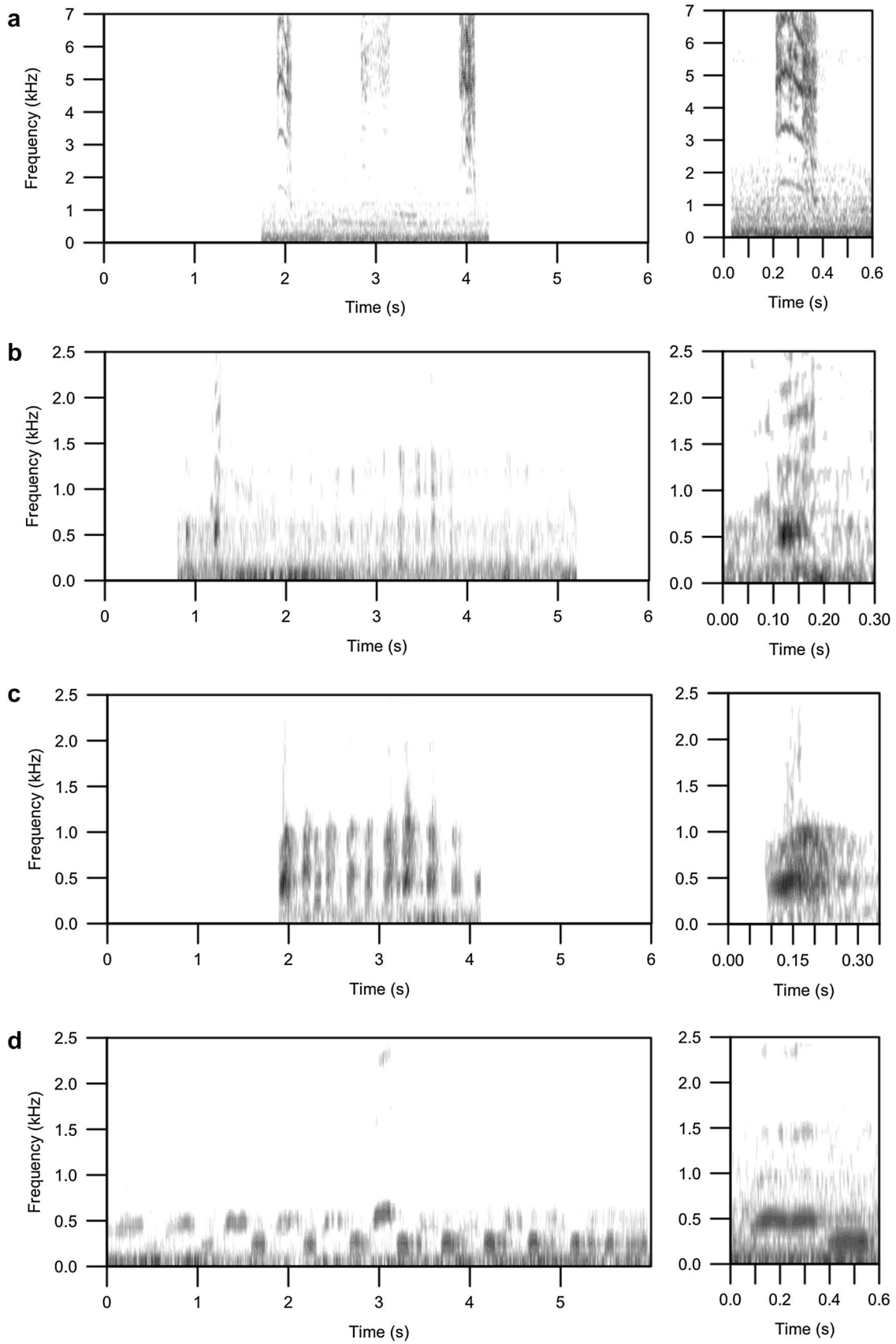
respectively. We presented three participants with one of the four unique Rough Grunt / Control Call stimulus pairs (Table 1). Audio of all stimuli are provided in the Supplemental Materials.

## Analysis

From video recordings of our trials, we coded the room the participants approached first during each trial. A participant was considered to approach a room if s/he walked towards the door of a room and peered inside and/or immediately entered the room. We also analyzed which room the participants fed in first, since participants did not always proceed to feed from the room they first approached. A participant was considered to feed in a given room if s/he consumed any food from that feeding site. For the Silence condition, we used two-tailed binomial tests to determine whether the proportion of participants that approached and fed first in the left (vs. right) rooms differed significantly from chance (0.5). The left and right designations were coded from the observer’s perspective looking towards the chimpanzee area from the human area (Fig. 1). For the Rough Grunt and Control Call conditions, we used two-tailed binomial tests to determine whether the proportion of participants that approached and fed first in the Stimulus (vs. Non-stimulus) Room differed significantly from chance. For a given trial in the Rough Grunt and Control Call conditions, the ‘Stimulus Room’ was considered to be the food presentation room from which a chimpanzee vocalization was broadcast, while the ‘Non-stimulus Room’ was the food presentation room from which a silent stimulus was broadcast.

Before each trial in the Rough Grunt and Control Call conditions, the observer randomly selected the side from which to present the stimulus and did not impose the constraint that the stimulus should be presented on the left and right sides in equal numbers of trials. Due to chance, the stimulus was presented on the right side in 8 out of 12 trials in the Rough Grunt condition and in 4 out of 12 trials in the Control Call condition (Supplemental Table 4). Since we found that more participants had a tendency to first approach the right room (see “Results” section) and more stimuli were presented from the right room in the Rough Grunt condition than the Control Call condition, we conducted additional analyses to disentangle any potential effects of side bias and stimulus presentation.

We examined the number of participants that first approached the left and right rooms in each trial type, regardless of the side from which a stimulus was presented, if any. To gain additional data points on participant behavior, we coded the participants’ behavior in their two training trials, which were comparable to the silent trials except that the door to the center room was not closed immediately after the participant entered during the first training trial and the





**Fig. 3** Spectrograms of the vocalizations used as stimuli in the Control Call condition, **a** Raspberry, **b** Pant grunt, **c** Pant grunt, **d** Pant hoot introduction. Letters a through d correspond to the Stimulus Pair ID listed in Table 1. Darker shades of grey represent louder relative amplitudes. The panels on the left display the full stimuli used for playback and the panels on the right show a close up of one vocalization from each stimulus. The right panel of 3d displays both an inhalation and exhalation. Note the higher y-axis values of **a** due to the higher frequencies present in this vocalization. Spectrograms were generated using the spectro function in *R* (version 4.0.5) with a window length of 512, an amplitude range of 40 dB at 5 dB intervals and overlap of 50% between successive analysis windows

observer did not discretely initiate the silent stimulus during either training trial.

We further examined each participant's behavior across their three non-stimulus trials (two training trials and Silence trial) to gain a greater understanding of their behavior without any potential influence of stimuli. We compared the number of participants that first investigated each room during non-stimulus trials to results generated from a simulation in which participants randomly chose a room to first approach on each of three turns (Supplemental Materials). In addition, we simulated an experiment that retains the observed number of times participants first investigated the left and right rooms and the number of times the rough grunt and control call stimuli were presented on the left and right sides while removing any relationship between these variables (Supplemental Materials). We replicated this simulation 1000 times and compared this null dataset to our observed data (Supplemental Table 3).

## Results

All 12 participants voluntarily and successfully completed all training and study trials. During the Control Call condition for participant 'KK', an adult male (Supplemental Table 1), 'KK' produced a pant hoot in response to the playback of a pant hoot by 'RE', another adult male in his group (Table 1). This response supports our expectation that the participants interpreted the acoustic stimuli as they would calls produced spontaneously by their group members.

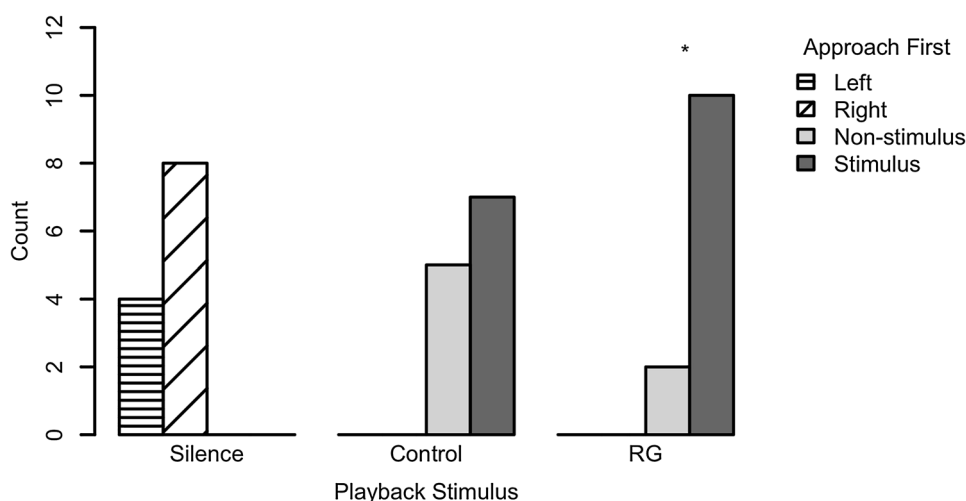
In the Rough Grunt condition, significantly more participants first approached the room from which rough grunts had been broadcast ("Stimulus Room") compared to the silent room ("Non-stimulus Room") (Stimulus:Non-stimulus (S:NS) = 10:2,  $P = 0.039$ , Fig. 4), supporting the hypothesis that rough grunts attract receivers. However, there was not a significant difference in the number of participants that chose to feed first in the Stimulus or Non-stimulus Room (S:NS = 6:6,  $P = 1$ , Fig. 5). In the Control Call condition, there was not a significant difference in the number of participants that approached or fed first in the Stimulus or Non-stimulus Room (Approach: S:NS = 7:5,  $P = 0.77$ , Fig. 4;

Feed: S:NS = 8:4,  $P = 0.39$ , Fig. 5). This finding suggests that participant reactions in the Rough Grunt condition are not simply due to the perceived presence of a familiar group member in the Stimulus Room. For a more detailed breakdown of participant responses, see Supplemental Figs. 1 and 2 which present participant responses to the different rough grunt and control call stimuli and a comparison of participant responses within each stimulus pair.

In the Silence condition, there was not a significant difference in the number of participants that approached or fed first in the right or left rooms [Approach: Right:Left (R:L) = 8:4,  $P = 0.39$ , Fig. 4; Feed: R:L = 7:5,  $P = 0.77$ , Fig. 5], indicating that there was not a significant side bias across participants. However, there was a tendency for more participants to first approach the right room than the left room. When we examined all trial types, we found that there was not a significant difference in the number of participants that first approached the left or right rooms in any trial type, though more participants first approached the right room in all trial types except for the first training trial (Training Trial 1: R:L = 6:6,  $P = 1$ ; Training Trial 2: R:L = 7:5,  $P = 0.77$ ; Silence: R:L = 8:4,  $P = 0.39$ ; Control Call: R:L = 7:5,  $P = 0.77$ ; Rough Grunt: R:L = 8:4,  $P = 0.39$ ; Supplemental Fig. 3).

When we focused only on participant behavior in their non-stimulus trials, we found that they first approached the right room in 58.3% of trials ( $n = 36$ ). In their three non-stimulus trials, 10 out of 12 participants first approached rooms on both the left and right sides at least once, 1 participant first approached the right room in all three trials and 1 participant first approached the left room in all three trials (Supplemental Fig. 4). 9 out of 12 participants first approached more rooms on the right side than the left side in their three non-stimulus trials. We found that our observed results were not significantly different than expected by chance, providing no evidence for a significant side bias across participants (Supplemental Table 2).

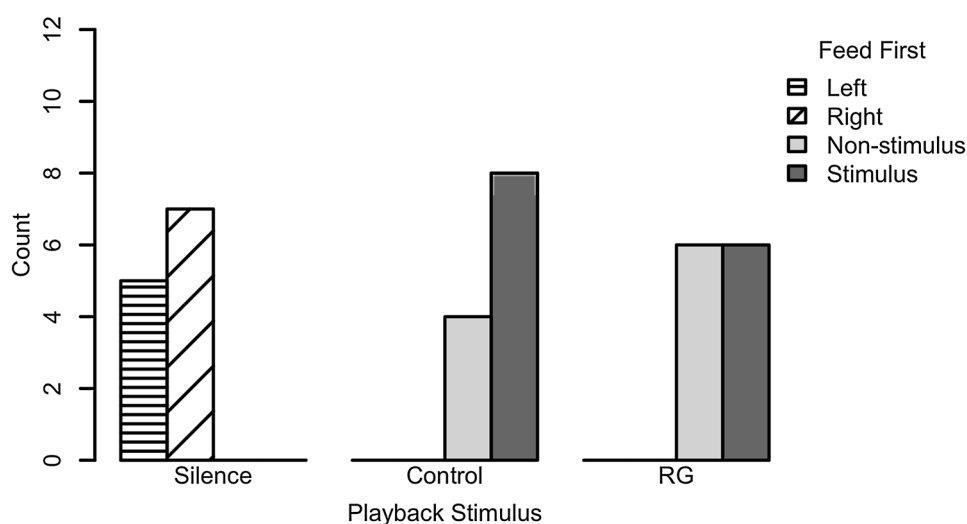
When we compared participant behavior in our study to that in our simulated study, we found that the number of participants that first approached the right room in the Silence condition was not significantly different in the observed data than the null dataset ( $P = 0.72$ ) indicating that our simulation captured participant behavior well in the absence of stimuli. The number of participants that first approached the stimulus room in the Rough Grunt condition was significantly greater in the observed dataset than the null dataset ( $P = 0.046$ ), supporting the hypothesis that this result was due to participants' attraction to the rough grunt stimulus and not simply due to subtle side biases and/or chance. In contrast, the number of participants that first approached the stimulus room in the Control Call condition was not significantly different from the null dataset ( $P = 0.58$ ), providing no evidence that the attraction response observed in the Rough



**Fig. 4** Bar plot displaying the number of participants that chose to first approach each room in each condition. The bars for the Rough Grunt and Control Call conditions represent the number of participants that visited the Stimulus vs. Non-stimulus Rooms, respectively. The bars for the Silence condition represent the number of indi-

viduals that visited the left vs. right room, respectively. The asterisk indicates that the number of participants that first approached the Stimulus vs. Non-stimulus Room during the Rough Grunt condition differed significantly from chance ( $P < 0.05$ )

**Fig. 5** Bar plot displaying the number of participants that chose to first feed in each room in each condition. The bars for the Rough Grunt and Control Call conditions represent the number of participants that visited the Stimulus vs. Non-stimulus Rooms, respectively. The bars for the Silence condition represent the number of individuals that visited the left vs. right room, respectively



Grunt condition was simply due to the perceived presence of familiar group members.

## Discussion

In our study, we sought to test whether rough grunts attract, repel or have no effect on the proximity of receivers in foraging contexts. We found that, more often than by chance, participants first approached the feeding site from which rough grunts were broadcast, rather than the silent feeding site. This approach behavior was not simply due to the perception that a familiar group member was present in the Stimulus

Room, since the vocalizations presented in the Control Call condition did not attract more participants than expected by chance. While there was a non-significant tendency for more participants to first approach the right room than the left room, the attractive effect we observed in the Rough Grunt condition was greater than expected, even when taking this tendency into account. Our findings support the hypothesis that rough grunts elicit an approach response from receivers. Despite substantial interest in the attractive nature of rough grunts, there has been mixed evidence regarding whether rough grunts attract receivers in the wild. One study found that the production of rough grunts upon arrival at a food patch correlated with the arrival of more extra-party

individuals for only one out of five tree species (Kalan et al. 2015). In addition, Kalan and Boesch (2015) found that rough grunt production correlated with the subsequent arrival of other foragers during feeding bouts involving fruit, but not feeding bouts involving nuts or leaves. Furthermore, they found that while sexually receptive females were more likely to be attracted to a food patch after an adult male produced rough grunts, such attraction did not occur when adult females produced rough grunts. One potential reason why previous studies have found mixed evidence for attraction while we found clear evidence for attraction is that our study focused on the approach of receivers at close range. Most studies in the field have focused on whether current or extra-party members enter the signaler's food patch (which often represents an entire tree) following call production (Kalan et al. 2015; Kalan and Boesch 2015). No field studies to date have examined the correlation between rough grunt production and changes in the proximity of nearby foragers relative to the signaler, though Fedurek and Slocombe (2013) did find that important social partners were more likely to remain in the vicinity after rough grunts were produced. By examining changes in receiver proximity in the wild surrounding the time of rough grunt production, similar to studies conducted with white-faced capuchins and pied babblers (Boinski and Campbell 1996; Gros-Louis 2004a; Radford and Ridley 2008), researchers could test the results of our study and shed light on the impact rough grunts have on receiver proximity in the wild.

The results of our study did not provide any support for the hypothesis that rough grunts repel receivers. If rough grunts repel others, we predicted that receivers would first approach the silent feeding site during the Rough Grunt condition. Rather, we found the opposite response. Thus, we found no evidence that rough grunts function similarly to the repellent food-associated vocalizations of some species (Boinski and Campbell 1996; Gros-Louis 2004a; Radford and Ridley 2008). Some studies have found that receivers will approach repellent food-associated (or agonistic) calls since they may still provide contextual information about the presence of a food source (Gros-Louis 2004b; Heinrich and Marzluff 1991; Jiang et al. 2016). We designed our study to reduce this possibility by familiarizing the participants with the presence and equal quality of both feeding sites during training trials and providing participants with the opportunity to view both food sources at the start of each trial. Thus, we consider it unlikely that participants approached the Stimulus Room because they perceived it was their only chance for acquiring food.

Researchers have commonly assumed that rough grunts elicit an approach response in receivers due to the information they provide about the presence and/or properties of the food source (Clay et al. 2012; Goodall 1986; Kalan et al. 2015; Slocombe and Zuberbühler 2005, 2006). As

mentioned above, we designed our study to reduce uncertainty regarding the presence and quality of food in the two rooms. Indeed, results of our study indicate that participants were not more likely to feed first from the Stimulus Room in the Rough Grunt condition, supporting the interpretation that participants did not view this feeding site to be higher quality. However, since participants were not able to view the inside of either food presentation room before or during the playback, it is possible that participants associated the rough grunt playbacks with the presence of an additional food source. While there is not strong support for the hypothesis that rough grunts convey detailed information about discovered food, field studies have found evidence that the likelihood of production and acoustic properties of rough grunts correlate with broad food patch characteristics, such as food class (e.g. ripe fruit, young leaves) or patch size (Fedurek and Slocombe 2013; Kalan et al. 2015). The only prior study involving playbacks of rough grunts suggests that the acoustic properties of rough grunts can inform listeners about the availability of specific foods, enabling receivers to focus their foraging efforts on those food patches (Slocombe and Zuberbühler 2005). However, as that study was only conducted with a single individual in captivity, it is unclear whether these results are generalizable to other individuals and/or contexts. Nevertheless, a follow-up study would need to be conducted in order to rule out whether chimpanzees have specific expectations about the presence and properties of a food source upon hearing different rough grunt vocalizations.

An alternative reason for why broadcasts of rough grunts attracted listeners may be that they advertise the signaler's motivation to forage for a long period of time in a particular location, information that could help promote behavioral coordination among group members. In a study testing this hypothesis, Fedurek and Slocombe (2013) found that rough grunt production by wild chimpanzees was correlated with longer feeding bouts by the signaler. Furthermore, when an adult male produced rough grunts, his important social partners were more likely to remain in the vicinity of the food patch, and chimpanzees that remained silent while foraging fed longer when others in their party produced rough grunts (Fedurek and Slocombe 2013). Thus, rough grunt production could help signalers retain important group members in the vicinity of the food patch since chimpanzees (Georgiev et al. 2014) and other species (Alberts et al. 1996; Kazahari 2014) can experience a tradeoff between maximizing foraging efficiency and maintaining spatial proximity. Attracting receivers towards the signaler could be one mechanism through which rough grunts help retain these individuals in the vicinity (Kalan and Boesch 2015).

Another reason why rough grunts elicited an attractive response could be that rough grunts advertise an affiliative motivational state to fellow foragers, facilitating co-feeding

at food patches. Chimpanzees can display high levels of food-related competition and aggression in foraging contexts (Goodall 1986; Houle and Wrangham 2021; Wittig and Boesch 2003). Therefore, the production of an affiliative vocalization could signal that foragers are receptive to others approaching to co-feed (Ischer et al. 2020). Encouraging others to co-feed at an abundant food patch could be beneficial for both signaler and receiver, since it could reduce the risk of predation (Elgar 1986b), deter others from seizing the food patch (Heinrich 1988), promote social opportunities such as mating (Kalan et al. 2015), and/or retain the proximity of more adult males for purposes of intergroup competition (Wilson et al. 2007). Similarly, by advertising a reduced likelihood of challenging others, signalers could potentially reduce the chances that they, themselves, will receive aggression, as was observed in white-faced capuchins and rhesus macaques (*Macaca mulatta*) (Gros-Louis 2004a; Hauser and Marler 1993). The hypothesis that rough grunts advertise an affiliative motivational state while foraging is congruent with previous findings that chimpanzees are more likely to produce rough grunts in the presence of close social partners, sexually receptive females and high-ranking individuals (Fedurek and Slocombe 2013; Kalan and Boesch 2015; Schel et al. 2013) as well as after the occurrence of agonistic interactions (Ischer et al. 2020).

While the results of our study cannot determine why participants approached the stimulus, at minimum, their approach response indicates that rough grunts attracted the participants' attention and that they felt comfortable enough to increase proximity to the signaler. In fact, simply attracting the visual attention of receivers could be enough to share information regarding the signaler's behavior and/or the presence and properties of the food patch. One reason why the rough grunt playbacks may not have caused more participants to feed first from the Stimulus Room could be because the treatment effect was eliminated once participants approached the stimulus and saw that there was no chimpanzee present and/or that the food in this room was no different than the food presented at the beginning of the experiment. Another limitation of our study is that, due to our use of multiple control call types, we were not able to determine whether rough grunts are more attractive than certain species-specific vocalizations. Ideally, all participants could be tested with multiple control call types so that responses can be compared across participants and across different call types. Additional captive playback studies would need to be conducted to test the effect of rough grunt production against that of particular species-specific vocalizations.

Overall, more studies are needed that test the effect rough grunts have on receiver behavior, especially in wild populations. Conducting field playback experiments would be especially useful. Field playback experiments have been

successfully conducted with wild chimpanzee pant hoots (Herbinger et al. 2009; Wilson et al. 2001), including a study investigating the effect a chimpanzee's simulated arrival has on the rough grunt production of receivers (Schel et al. 2013). While playbacks of close range vocalizations, such as the rough grunt, are more logistically difficult, they have been successfully conducted in other primate species (e.g. Engh et al. 2006; Rendall et al. 1999). In addition to playback experiments, observational field studies can continue to shed light on the function of rough grunts. While early studies tended to focus on the potential for rough grunts to function referentially, studies have more recently begun to examine the correlation between rough grunt production and receiver behavior (Fedurek and Slocombe 2013; Ischer et al. 2020; Kalan et al. 2015; Kalan and Boesch 2015), including the role these calls may play in mediating social interactions while foraging (Fedurek and Slocombe 2013; Ischer et al. 2020). Together, both experimental and observational studies can help shed light on the effects rough grunts have on receivers and how these changes in behavior impact signalers.

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## Declarations

**Ethical standards** All procedures performed in these studies adhered to the ethical standards in the protocols approved by the IACUCs of The University of Texas MD Anderson Cancer Center (UTMDACC) and the University of Minnesota (Protocol number # 1002A78194). The authors declare that they have no conflict of interest.

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