RESEARCH ARTICLE

Do chimpanzee food calls bias listeners toward novel items?

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Abstract

Social learning is beneficial in almost every domain of a social animal's life, but it is particularly important in the context of predation and foraging. In both contexts, social animals tend to produce acoustically distinct vocalizations, alarms, and food calls, which have remained somewhat of an evolutionary conundrum as they appear to be costly for the signaller. Here, we investigated the hypothesis that food calls function to direct others toward novel food items, using a playback experiment on a group of chimpanzees. We showed chimpanzees novel (plausibly edible) items while simultaneously playing either conspecific food calls or acoustically similar greeting calls as a control. We found that individuals responded by staying longer near items previously associated with food calls even in the absence of these vocalizations, and peered more at these items compared with the control items, provided no conspecifics were nearby. We also found that once chimpanzees had access to both item types, they interacted more with the one previously associated with food calls than the control items. However, we found no evidence of social learning per se. Given these effects, we propose that food calls may gate and thus facilitate social learning by directing listeners' attention to new feeding opportunities, which if integrated with additional cues could ultimately lead to new food preferences within social groups.

KEYWORDS
ape, foraging, social facilitation hypothesis, social learning, vocalization

1 | INTRODUCTION

Social learning, defined as instances of learning from watching or interacting with others or their products (Heyes, 1994), is widespread in social animals and especially well-studied in the domain of object manipulations (Davis & Whiten, 2018; Whiten & Ham, 1992; Whiten, 2005). Social learning is thought to evolve when individual learning by trial and error is costly, for example, if learning opportunities are rare, restricted to high-risk situations, and/or likely to lead to harmful errors (Galef & Giraldeau, 2001; Laland, 2004). Although social learning may be beneficial in almost every domain of a social animal's life, it should be particularly important in the context of predation and foraging. In both contexts, young individuals are confronted with a large number of animal and plant species and have to learn quickly and reliably to discriminate the harmless from the dangerous. Benefitting from others' knowledge is clearly a very

effective way of acquiring such knowledge. Regarding predator recognition, primates (and other animals) appear to possess core knowledge about basic natural categories of dangers (aerial vs. terrestrial), allowing them to gradually exclude harmless species by observing the reactions of more experienced group members (Seyfarth & Cheney, 1980, 1986). Social learning of predator recognition appears to be extremely rapid and efficient, in some cases only requiring single exposures (Blum et al., 2020; Curio et al., 1978a, 1978b; Wegdell et al., 2019).

In all likelihood, social learning also plays a major role in acquiring foraging competencies but here the challenge is considerably larger, especially for generalist feeders (Galef & Giraldeau, 2001). For example, wild chimpanzees, *Pan troglodytes*, consume hundreds of different plant items, all of which have to be identified individually and discriminated against a background of thousands of unpalatable and sometimes toxic foods (Matthews et al., 2019; Newton-Fisher et al., 2000). Correspondingly, social learning of foraging behaviors has been demonstrated in a wide range of taxa, such as rodents (Galef, 1996; Galef & Henderson, 1972), birds (Allen & Clarke, 2005; Nicol, 2004; Sherwin et al., 2002), fish (Laland & Williams, 1997; Pike & Laland, 2010), and primates (Hikami et al., 1990; Hopper et al., 2011; O'Mara & Hickey, 2012; Shorland et al., 2019; van de Waal & Whiten, 2012; van de Waal et al., 2010, 2013).

Although the biological function of social learning in the acquisition of foraging behavior is well established and undisputed, comparably little is known about the cues naïve individuals use to learn from more experienced ones. Clearly, direct observations are likely to play an essential role, but naïve animals would benefit strongly if experienced animals produced signals or otherwise ostensive behaviors whenever learning opportunities arise. While any social cue produced during a learning opportunity would suffice, there is evidence that vocalizations play a special role in enabling and facilitating social learning (Curio, 1978; Curio et al., 1978a, 1978b; Rendall et al., 2009; Vieth et al., 1980). For example, in the predator-avoidance domain, there is evidence that calls alone can trigger learning (Griffin, 2004), as first demonstrated in blackbirds that socially learn to avoid other species, simply from perceiving others' mobbing vocalizations (Vieth et al., 1980).

Whether or not vocalizations play a similar role in the acquisition of foraging competencies is less well-studied. Although limited, there are some accounts in which vocalizations may be social triggers of learning. One potential example is the social transmission of food preferences in white-tailed ptarmigans (*Lagopus leucurus*). Here, field experiments demonstrated that mothers preferentially produced multimodal titbit displays in the presence of palatable foods with calling rates related to chick food preferences (Allen & Clarke, 2005; Clarke, 2010). Stronger evidence comes from cotton-top tamarins (*Saguinus oedipus*), which produce a distinct type of food vocalization that is directed at juveniles and elicits approach behaviors and taking of the food offered (Joyce & Snowdon, 2007; Roush & Snowdon, 2001). Food avoidance also appears vocally aided by the increase in alarm calls and decrease in food call (FC) production in this species (Snowdon & Boe, 2003). Yet, the currently limited evidence is in stark contrast to the wealth of data indicating that many animals, including mammals (Clay et al., 2012) and birds (Marler, 2004), produce acoustically distinct vocalizations (termed "food calls") when encountering food or while feeding. Chimpanzees also produce FC (i.e., "rough grunts," Goodall, 1986), which are referential in the sense that the acoustic structure of the grunts varies with how the caller perceives the quality of the food, which listeners attend to for foraging decisions (Slocombe & Zuberbühler, 2005, 2006). Chimpanzee FC also have a strong social component (Taglialatela et al., 2012), with individuals being more likely to call when socially bonded or dominant individuals are nearby (Kalan & Boesch, 2015; Slocombe et al., 2010). Nevertheless, the function of food calling is still debated, with two main hypotheses: either FC inform others competitively about food ownership (Gros-Louis, 2004) or cooperatively about exploitable food patches (Schel et al., 2013; Slocombe et al., 2010). In chimpanzees, both functions may play a role simultaneously, since individuals are more likely to call both after the arrival of bonded individuals and when levels of aggression in the feeding event are high, suggesting that FC also mitigates aggression (Ischer et al., 2020).

In this study, we were interested in a potentially novel function of chimpanzee FC:

Facilitating, or gating, social learning of foraging behaviors. In a recent study with chimpanzees, we partially addressed the social facilitation learning hypothesis by showing that naïve animals were faster at learning a visual discrimination task (leading to food rewards) if they were primed with FC compared with other calls (Déaux et al., 2021). We concluded that FC may enhance the attention of listeners and thus enhance their ability and readiness to learn novel visual information.

To test the hypothesis that chimpanzee FC function as learning aids for the foraging behavior of other group members, we repeatedly exposed a whole chimpanzee group to two novel items (cotton objects) in the presence of FC (rough grunts) or acoustically similar greeting calls (GC) (pant grunts). We then compared subjects' subsequent behavioral responses toward the novel items, following exposure to the two call types, while controlling for social influences. We predicted that, if FC served as gating signals, individuals should show a greater readiness to explore the novel items previously associated with FC than those initially associated with the GC.

2 | MATERIALS AND METHODS

2.1 | Ethical statement

All procedures performed in this study were in accordance with the laws of Switzerland and the ethical standards of the canton (Kantonales Veterinäramt Basel Stadt, permit number 2861).

2.2 | Subjects and study site

The study was conducted with chimpanzees, *P. troglodytes* versus, housed at Basel Zoo, Switzerland. During the experimental data

collection period (24/05/2019–05/06/2019), the group consisted of 13 individuals; 3 adult males, 6 adult females, 1 juvenile female, 1 infant male, and 2 infant females. All individuals were part of a cohesive social group, had access to four indoor (totaling 1030 m³) and two outdoor enclosures (totaling 3900 m³), and were fed a mix of fruits and vegetables supplemented with protein several times per day with continuous access to water. We collected data on 10 of the 13 individuals who participated in the study (age range: 5–51 years), excluding the three infants who were still dependent on their mothers. Animals could not be separated for the experiments due to zoo regulations, such that we established an experimental design where all individuals were tested simultaneously, as a group.

2.3 | Acoustic stimuli

FC and GC recordings were obtained from an adult male unfamiliar to the subjects ("Kwezi") from the Sonso community of Budongo Forest, Uganda (Figure 1b). Although we do not know what food elicited the FC, we ensured that the selected call did not include any food-related (e.g., chewing, cracking/smacking noises) background noise. We used GC as control vocalizations because, within the chimpanzee vocal repertoire, both call types belong to the same category of "grunt" vocalizations such that their spectro-temporal features (i.e., grunt sequences) are similar, yet their use and function are different (Boesch & Crockford, 2005; Goodall, 1986).

We chose to present calls from an unfamiliar individual to avoid complications when playing the calls of familiar individuals being

physically present inside the enclosure. Chimpanzees recognize each other by voice (Martinez & Matsuzawa, 2009), suggesting that broadcasting calls from familiar individuals would have been confusing, given the impossibility of removing or separating individuals at Basel Zoo. Presenting unfamiliar vocalizations from outside the enclosure was a more plausible scenario (see Keenan et al., 2016) because group members have previously experienced new individuals being added to the group, as part of the zoo's husbandry program (McClung et al., 2020). Furthermore, we only used calls from one chimpanzee for ethical reasons, as simulating the introduction of multiple individuals might have raised stress levels in the resident chimpanzees (Yamanashi et al., 2016). The FC series included 15 calls and lasted 7.6 s, while the GC series included 20 calls and was 6.6 s long. We used the seewave R package (Sueur et al., 2008) to extract the call duration and the first two frequency peaks and compared these characteristics to those previously reported. The acoustic features of FC are within the range of values reported for wild chimpanzees (Table 1) (Kalan et al., 2015). GC have been described as having elements of 30–200 ms and frequencies concentrated below 1.5 kHz, typically around 100–500 Hz (Boesch & Crockford, 2005; Marler & Tenaza, 1977), such that the GC used in this study roughly concord despite being slightly over the range.

The GC were recorded in February 2019, using a shotgun microphone Sennheiser ME66 with power module K6 and a portable recorder Marantz Pro PMD661. The FC were recorded in February 2017, using a shotgun Sennheiser MKE600 microphone and a Marantz PMD620 recorder. While the recording equipment are different, the frequency responses of the two microphones are the
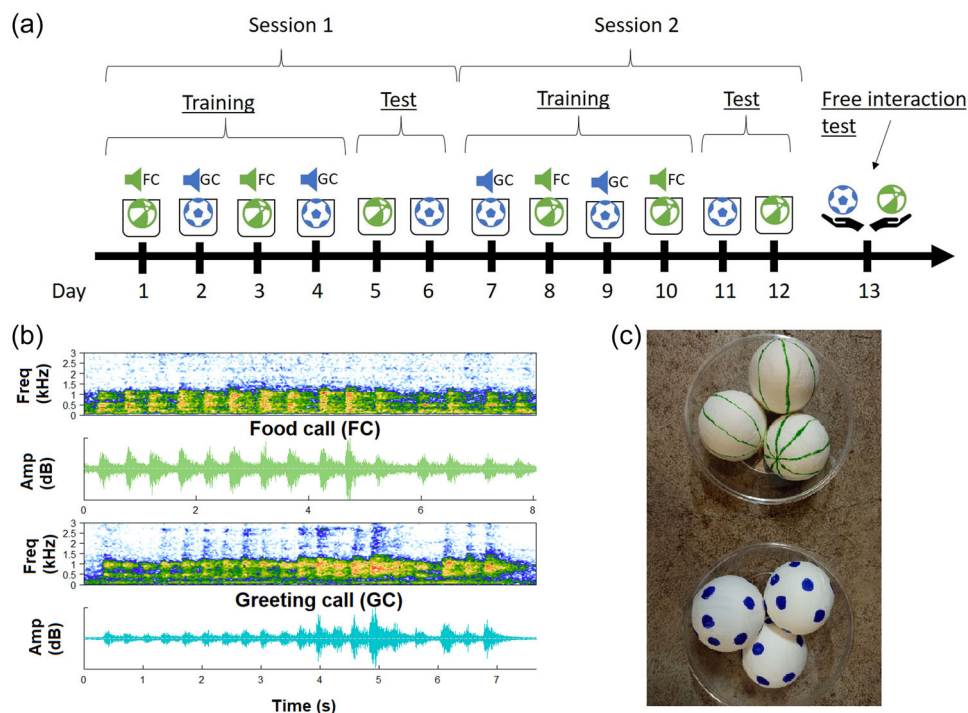

FIGURE 1 Experimental procedure. (a) Diagram of the timing of the experiment. (b) Spectrograms (DFT = 1024, ovlp = 0, Hanning window) and waveforms of the food call (top half) and greeting call (bottom half) used as acoustic stimuli. (c) picture of the novel items used.

	Duration (ms)	DF1 (Hz)	DF2 (Hz)
Food calls			
This study	280.97 ± 38.23	264.14 ± 91.52	620.16 ± 183.93
Kalan et al. (2015)	173.77–290.54	171.74–330.76	344.28–663.08
Greeting calls			
This study	211.48 ± 30.09	516.80 ± 136.19	1033.59 ± 400.31
Boesch & Crockford (2005), Marler and Tenaza (1977)	30–200	~100–500	<1500

TABLE 1 Summary statistics (mean ± SD) of call acoustic characteristics used in this study as compared with published accounts (ranges given).

same, the main difference between the two pertaining only to their level of self-noise, which is unlikely to bear an impact considering that these were recordings made in the wild. Using Audacity (https://www.audacityteam.org; v 2.3.1), we filtered (high-pass filter 100 Hz) and normalized the recordings in amplitude. We created stimulus tracks of approximately 150 s containing five repetitions of the FC or GC series separated by 30 s of silent interval. We considered that these calls would be meaningful to the Basel Zoo chimpanzees given that they all regularly produce and hear FC and GC.

2.4 | Novel items

Because we had to test all individuals together, this meant that we could not randomly assign chimpanzees to different treatment conditions. Another way to control for a potential item bias would have been to rerun the experiments with alternate pairings, or to test their preferences of the two items before pairing them with vocalizations. However, had we done so, the items would not have been new such that from individual knowledge chimpanzees would have been aware of the nonpalatability of the items and in the case of a second run there could have been carry-over effects that could affect the pattern of responses. Due to these limitations, we instead decided to run only one experiment with two fixed item vocalizations pairings but to select items that were the least likely to elicit different initial preference biases. Both novel items had identical shapes, that is, being commercially available cotton balls (4 cm diameter; Cultura), on which we drew either green lines or blue points (Figure 1c). Color preference can influence learning (Roy et al., 2019) as such, we selected colors that chimpanzees can discriminate (Buchanan-Smith, 2005) without showing any preference bias (Wells et al., 2008). Similarly, we chose lines and dots patterns as they are easily distinguishable patterns (Hegdé & Van Essen, 2000). The items were then randomly assigned to one vocalization, that is, chimpanzee FC were paired with green-lined items (henceforth termed "FC-associated item") whereas GC were paired with blue-dotted items (henceforth termed "GC-associated item"). Whether either type of item could have been perceived by the chimpanzees as bearing a resemblance with known edible fruits such as cantaloupes or blueberries, which could have induced a preference bias is unknown. However, control analyses (see Section 3) suggest that there was no such initial bias.

2.5 | Experimental design

As the chimpanzees could not be separated for the tests, we tested the whole group together each time. The experiment included two sessions, each consisting of a 4-day training phase, followed by a corresponding 2-day test phase (12 days total), to account for random daily variation in individual behaviors (Figure 1a). We conducted one trial per day (either FC or GC condition), using an alternating schedule, after having randomly selected the treatment condition for the very first trial. We reversed the presentation order in the second session. On the 13th day, we conducted a final assessment in which the individuals were finally given access to the two item types.

Both training and test phases started around 10:00 after the first meal of the day, which was normally given around 09:30 local time. A training phase consisted of chimpanzees being presented with three cups separated by 20 cm from each other, each containing three items. Items were inaccessible but visibly positioned on the ground outside the enclosure. Once the set-up was completed, the experimenter left the room and the playback of the paired acoustic condition (i.e., GC for GC-associated items, FC for FC-associated items) started 2 min after. Calls were broadcasted using a Premio 8.2 speaker (T.A.G.) at approximately 75 ± 5 dBC. The speaker was placed in a fenced-off enclosure, approximately 1 m behind the cups and hidden behind a tarp as to make it plausible that an unfamiliar chimpanzee would be present in the building (see Supporting Information: Figure 1). Following the playback, the items were left in place for another 60 min while all vocal and nonvocal behaviors were recorded by three cameras (Pentax K-50, GoPro 3, Panasonic camcorder) and a Sennheiser MKE600 microphone plugged into a Marantz PMD620 solid state recorder. After that, the items and recording equipment were removed. Test phases were performed to record chimpanzees' behavioral responses to the items following exposure to the call-item pairings, as according to our hypothesis, FC should induce greater interest in the items compared with GC following exposure to the item-call pairings. Thus, they consisted of the same setup, that is, the items were positioned in exactly the same way for the same duration, but this time without any vocalizations being played back.

Once both sessions were completed, on the 13th day, we carried out a posttraining, free interaction test, which started around 11:00 local time and consisted of a two-choice task during which a keeper presented a choice of one FC-associated item and one GC-associated item simultaneously to each chimpanzee, followed by a 30 min period

of free interaction with the items. The Chimpanzee testing order was opportunistic, based on the order in which they came after being called over. For the two-choice task, the items were hand-held (right/left side randomly determined) and presented through the mesh at the chimpanzee's eye level. After initial inspections, subjects usually dropped the (inedible) items inside the enclosure leading to an increasing number of items scattered throughout the enclosure that individuals could freely interact with. To keep the number of FC-associated and GC-associated items comparable inside the enclosure, the keeper maneuvered the nonselected item into the enclosure following each choice. We documented all interactions with the items for a period of 30 min.

2.6 | Coding of behavioral responses

From the videos, during training and test phases, the following behaviors were scored: affiliative and agonistic behaviors, looks, stares, staying close, object throws, attempts to grab with hand, attempts to grab with a stick, vocalizations in direction of the items, and finally vocalizations next to the items (see Supporting Information: Table S1 for definitions). For the posttraining, free interaction test, we scored every individual's first choice (FC-associated vs. GC-associated) and the following behaviors for subsequent interactions with items already in the cage (see Supporting Information: Table S2 for definitions): grab with hand, put in the mouth, touch with hand, touch with a stick. Behavioral scoring was performed by one person who was blind to the condition, using BORIS (https://www.boris.unito.it; v 7.9.8).

2.7 | Behavioral response variables

2.7.1 | Training and tests phases

Following visual inspection of the frequency of behaviors displayed (Figure 2a), we found that, of all the behaviors scored, only two occurred at frequencies sufficiently large for statistical analyses: staying in close proximity to the items (hereafter "proximity" in seconds) and peering at the items (which included both "look" and "stare" responses; Schuppli et al., 2016).

Proximity response
Duration of proximity to the items, defined as an individual remaining within 3 m of the items was coded from the starting time of the behavior to when the individual moved away (in seconds). This variable was log-transformed for statistical analysis due to its right-skewness, to improve the normality and homoscedasticity of the statistical model's residuals.

Latency to approach
To test whether acoustic treatments attracted or repelled individuals (relative to the other treatment), we used the starting time of the first
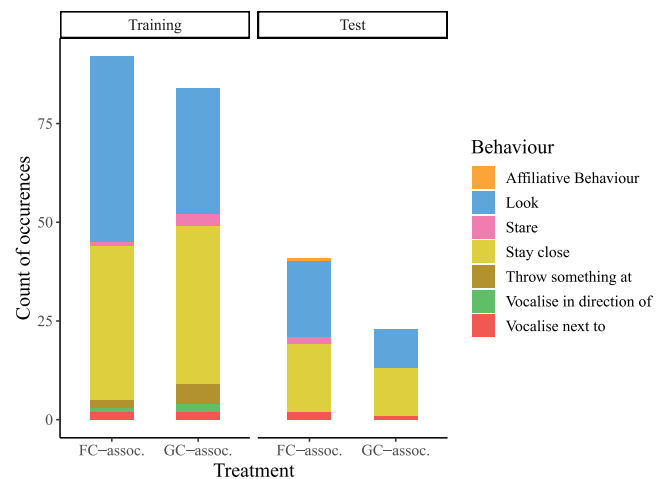

FIGURE 2 Frequencies of each behavior scored and their distribution according to the treatment (FC vs. GC) and the experimental phase (training vs. test) in which they occurred. FC, food calls; GC, greeting calls.

time an individual came in proximity of the items after acoustic stimulus onset (training phase only, as no acoustic stimulus was presented during test days) to obtain a latency measure (in seconds). This variable was also log-transformed for statistical analysis due to its right-skewness, to improve normality and homoscedasticity of the statistical model's residuals.

Peering response
The peering variable included both "look" (defined as a gaze toward the item for <1 s) and "stare" (defined as a gaze >1 s) responses. Look responses being so short, it was difficult to quantify their duration yet they were much more frequent than stares (Figure 2a). Thus, to quantify peering we summed the counts of look and stare responses. We did this for each individual, per treatment, phase, and conspecific presence condition and then divided that value by the number of days in each phase (four for the training phase and two for the test phase), to correct for the difference in the number of training and test days.

Conspecific presence
Furthermore, as conspecific behaviors may affect an individual's response, we used conspecific presence as a proxy of social influences. Conspecific presence was coded as a binary variable, such that for each instance of proximity and peering behaviors, we coded whether at least one individual was already present in the vicinity or not (i.e., within 3 m of the items).

2.7.2 | Posttraining free interaction

To measure their level of interaction with the items, once those were freely available within their enclosure (thus after the two-choice test), we counted the number of times individuals investigated the items,

which could include grabbing the item and mouthing the item. We excluded the first interaction (choice in the two-choice task) from this count, instead adding the first choice in the statistical model to see if it would influence subsequent item investigation.

2.8 | Statistical analyses

2.8.1 | Training and tests phases

Proximity response

As not all individuals came in proximity to the items on every trial, we had unbalanced, replicated data. Thus, we built a linear mixed model (LMM) fit by restricted maximum likelihood, including treatment type (FC vs. GC), the phase (training vs. test), the presence of a conspecific (yes/no), their two-way and three-way interaction as fixed effects, day as a covariate, and random intercepts among subjects. The statistical significance of fixed effects was assessed using F tests and the Kenward–Roger method of degrees of freedom approximation. Post hoc pairwise differences were assessed by simple contrast with Tukey correction. Visual inspection of plots showed that the normality and homoscedasticity of residuals and random effects assumptions were met.

Latency to approach

As we could not conduct initial preference tests for the items (as this would have resulted in the items not being novel anymore), there was a possibility that the preference patterns detected after the pairing training could be a reflection of a preference for one of the items rather than an effect of the acoustic treatment. Given that we found no difference in proximity behaviors between the two treatments during the training phase (see Section 3), this could either mean that there was no initial preference in the two items or that the FC had an effect opposed to the initial item preference. In other words, FC should "repel" chimpanzees' approaches. Although this is contra the literature (Kalan & Boesch, 2015), as indeed FC are thought to attract conspecifics by advertising food presence, given the unfamiliar status of the acoustic exemplar, this remains a possibility in this experiment. To investigate whether FC repelled chimpanzees, we tested whether the latency to approach within 3 m of the items differed between treatments during the training phases. We used a linear regression model, adding an interaction between treatment and day, and conspecific presence and subject as a fixed effect (as treating the subject as a random effect resulted in a singular fit). Post hoc pairwise slope differences were assessed by simple contrast with Tukey correction.

Peering response

To investigate whether acoustic treatment influenced peering behaviors, we built an LMM fit by restricted maximum likelihood, including treatment type (FC vs. GC), the phase (training vs. test), the presence of a conspecific (yes/no), their two-way and three-way interaction as fixed effects and random intercepts among subjects.

Post hoc pairwise differences were assessed by simple contrast with Tukey correction.

2.8.2 | Posttraining free interaction

We used a binomial test to assess whether the number of first choices (FC-associated vs. GC-associated) occurring during the two-choice task was different from chance. Then, we built a generalized linear mixed model (GLMM) with a Poisson distribution with item type (FC-associated vs. GC-associated) and first choice as fixed effects and subject as a random term. Statistical significance tests of fixed effects were assessed using Wald χ^2 tests. The deviance test confirmed that the dispersion parameter was not significantly different from 1 ($\chi^2 = 9.91$, $p = 0.7$).

Statistical analyses and plots were performed in R version 3.5.1, using the packages: ggplot2 (Wickham, 2016), lme4 (Bates et al., 2015), lmerTest (Kuznetsova et al., 2017), plyr (Wickham, 2011), and emmeans (Lenth, 2019).

3 | RESULTS

3.1 | Training and tests phases

During both the training and test phases, we observed seven different behaviors among which only peering behaviors and staying close (i.e., "proximity") occurred frequently enough for statistical analyses (Figure 2a). We computed the peering response by including both look occurrences (number of observations: $FC_{training} = 47$, $FC_{test} = 19$, $GC_{training} = 32$, $GC_{test} = 10$) and stare behaviors ($FC_{training} = 1$, $FC_{test} = 2$, $GC_{training} = 3$, $GC_{test} = 0$). Of note, behaviors that would be suggestive of treatments having differing impacts on arousal or emotional valence (e.g., affiliative behaviors, throwing things or vocalizing), were seldom produced as for instance, grooming almost never occurred (one instance), and more generally such behaviors occurred at similar levels in both treatments (Figure 2a).

3.1.1 | Proximity response

For proximity, there was a significant interaction between treatment and phase ($F_{1,95.3} = 8.67$, $p = 0.004$); all other effects were non-significant (all $F < 3.1$, $p > 0.05$). During the training phase, there was no significant difference in the amount of time spent in proximity to the items between the GC treatment and the FC treatment ($t = 1.61$, $p = 0.11$) while, conversely, during the test phase, chimpanzees stayed in proximity to the FC-associated items longer than GC-associated items ($t = -2.53$, $p = 0.01$). As seen in Figure 3b, chimpanzees spent less time in the proximity of the GC-associated items in the test compared with the training phase, that is, in the absence of vocalizations ($t = 2.57$, $p = 0.01$). Such a phase difference was not present for the FC treatment ($t = -1.74$, $p = 0.08$). In other words, in
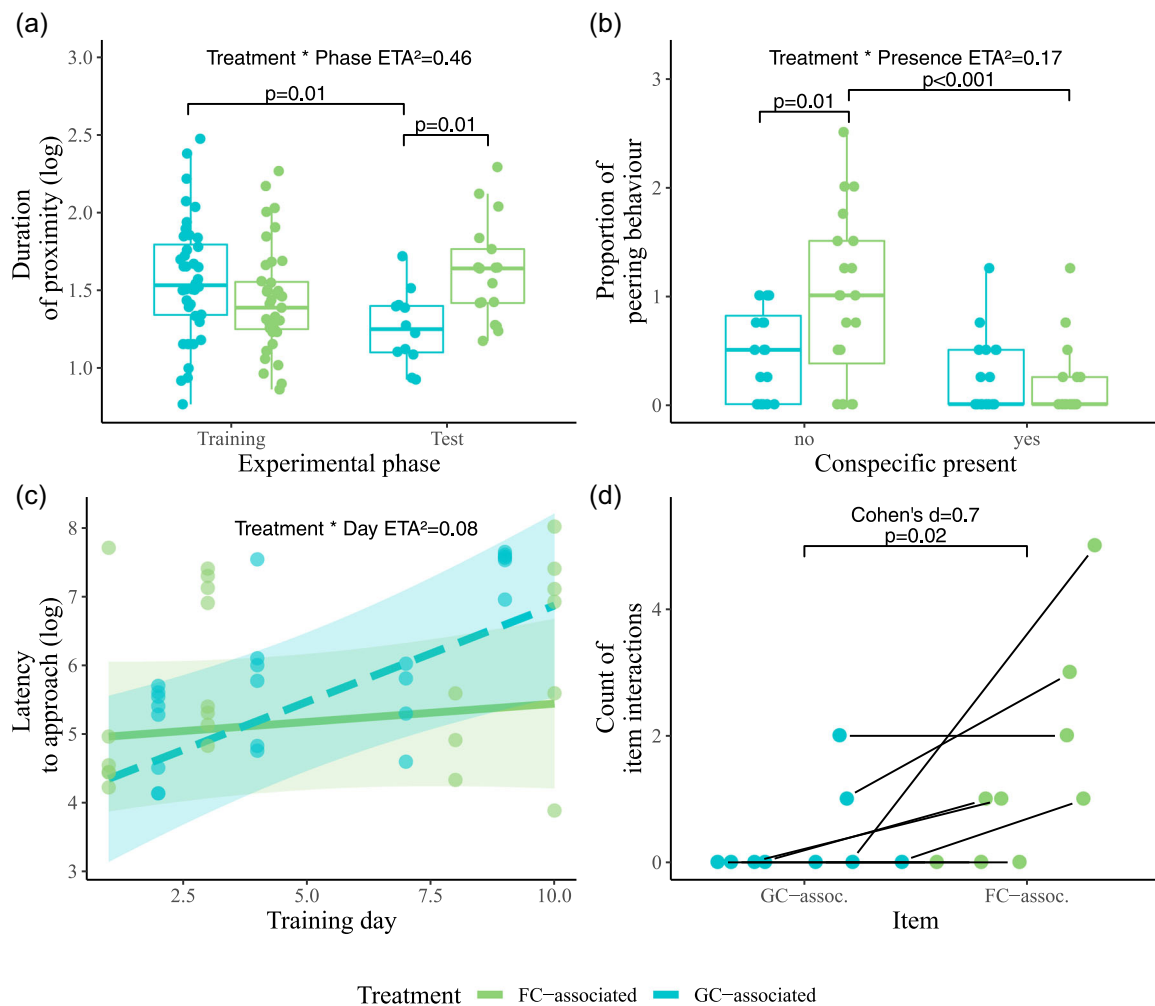
FIGURE 3 (a) Distribution of the duration of proximity (log-transformed) depending on treatment and experimental phase. Shaded areas are 95% confidence intervals. (b) Distribution of the proportion of peering events depending on treatment type and conspecific presence. (c) Latency (log-transformed) to approach in proximity of the items upon hearing FC or GC vocalizations as a function of training day. (d) Number of interactions with the items for each chimpanzee (N = 9). Data points have been horizontally dodged to ease visualization. FC, food calls; GC, greeting calls.

the absence of vocal signals, chimpanzees still remained in close proximity to the FC-associated items but not to the GC-associated items (Figure 3b). LMM results are provided in Supporting Information: Table S3.

3.1.2 | Latency to approach during training

When testing whether acoustic treatments differed in their attraction levels, we found a significant interaction effect of treatment and day on the latency to approach ($F_{1,33} = 4.45$, $p = 0.04$) and a main effect of the day ($F_{1,33} = 10.60$, $p = 0.002$) but not of treatment ($F_{1,33} = 0.11$, $p = 0.74$), conspecific presence ($F_{1,33} = 0.22$, $p = 0.42$) nor subject ($F_{9,33} = 1.05$, $p = 0.42$). The Post hoc test of the difference in the slopes showed a stronger positive slope for the GC condition than for the FC condition (FC-GC = −0.23, $t = -2.11$, $p = 0.04$). In other words, chimpanzees were slower to approach upon hearing a vocalization as

training progressed and this effect was more pronounced in the GC condition, suggesting that FC did not repel chimpanzees (Figure 3b,c).

3.1.3 | Peering response

We found that there was a significant interaction between the treatment condition and the presence of conspecifics ($F_{1,63} = 6.91$, $p = 0.01$) and significant main effects for treatment ($F_{1,63} = 4.18$, $p = 0.04$) and conspecific presence ($F_{1,63} = 23.51$, $p < 0.001$). Peering did not vary across phases either as a main effect ($F_{1,63} = 1.5$, $p = 0.22$) or as an interaction (all $F_{1,63} < 2.2$, all $p > 0.05$). As seen in Figure 3b, post hoc pairwise tests showed that, in the absence of conspecifics, chimpanzees peered more in the FC condition than in the GC condition ($t = -3.31$, $p = 0.002$), while there was no difference in peering between the two conditions, when conspecifics were nearby ($t = 0.41$, $p = 0.68$). Within conditions, conspecific presence

did not impact peering in the GC treatment ($t = 1.57$, $p = 0.12$), while they were less likely to peer when conspecifics were present in the FC treatment ($t = 5.29$, $p < 0.001$). Thus, chimpanzees peered more in direction of the items in the FC condition than the GC condition (regardless of the phase) but only in the absence of conspecifics. In the presence of conspecifics, peering was low regardless of treatment and phase condition. LMM results are provided in Supporting Information: Table S4.

3.2 | Posttraining free interaction

During the final assessment, we recorded, for each subject his or her first choice of the two available items. One individual never interacted with any of the items. Of the nine remaining individuals, six chose the GC-associated item while three selected the FC-associated item (binomial test: $p = 0.51$).

With regard to the amount of investigation of the freely available items, we found that chimpanzees engaged more with FC-associated than GC-associated items ($\chi^2 = 5.09$, $p = 0.02$, Figure 3d) and that this was not influenced by their initial choice (two-way interaction: $\chi^2 = 0.13$, $p = 0.71$; main effect: $\chi^2 = 0.33$, $p = 0.56$). GLMM results are provided in Supporting Information: Table S5.

4 | DISCUSSION

We exposed chimpanzees to novel items in association with two grunt vocalizations that differ in their contexts of production and putative function(s), that is, rough grunts (food) or pant grunts (greeting). If these vocal-item pairings were interpreted differently by chimpanzees, then we expected that this would influence their subsequent interactions with the items and result in different behavioral responses in future encounters. In agreement with this hypothesis, we found that chimpanzees behaved differently in the test phase (only items present, no vocal stimulus) depending on the prior acoustic treatment. Specifically, they stayed in close proximity to the out-of-reach items previously associated with FC (FC-associated items), unlike items previously paired with GC (GC-associated items). These results suggest that chimpanzees formed different expectations from the FC pairing than the GC pairing, which led to different behavioral responses during the test phase.

One could argue that this difference could be due to an initial bias toward the green-colored (which was randomly paired with the FC) item unrelated to the acoustic treatment. Indeed, as we were unable to test initial items preferences (as this would have resulted in items not being novel anymore), nor could we test chimpanzees separately to counterbalance the item-vocalizations pairings, it is difficult to refute this possibility, however, three pieces of evidence suggest it to be unlikely. First, proximity to the items did not significantly vary during the training phase between the two treatments. If individuals did prefer one of the two items and did not pay attention to the calls, then there should have been a

difference even during the training phase. However, one could argue that chimpanzees may have initially preferred the green-colored, FC-associated item but that FC from an unfamiliar individual repelled them, essentially counteracting the initial preference bias. If FC did have such a repellent effect, then we could expect that fewer chimpanzees would come to investigate the items upon hearing FC vocalizations. This was not the case as out of 10 individuals only 1 never came toward the items when FC vocalizations were broadcast. Lastly, if individuals were ambivalent toward the item-call pairing they may come but take longer to approach. Thus, the latency to approach upon hearing the vocalizations should be longer in the FC compared with the GC condition. However, the analysis revealed an inverse trend. Chimpanzees showed increased latencies to approach as training progressed and this was even stronger in the GC, arguing against a repellent effect of FC.

There is compelling evidence that monkeys and apes rely on social information when developing their foraging skills (Rapaport & Brown, 2008). For example, chimpanzees conform to group preferences (Hopper et al., 2011), and switch diets according to what others consume (Vale et al., 2017). Clearly, conspecific cues, such as food consumption, allow them to gather information as to the potential palatability of novel items. However, chimpanzees also produce acoustic signals, that is, FC, which are known to recruit group members to food patches (Kalan & Boesch, 2015), guide foraging efforts (Slocombe & Zuberbühler, 2005), and according to the results of our recent companion study, improve visual discrimination in food-related tasks (Déaux et al., 2021). Thus, chimpanzee FC could either serve as gating cues that prepare for a learning opportunity (the social facilitation hypothesis) or as direct cues that trigger social-learned food preferences, similar to how alarm calls have been shown to trigger learning (Griffin, 2004). The results of our experiment are better aligned with the social facilitation hypothesis and provide no evidence that FC in themselves, results in fully-fledged, novel, socially-induced food responses. The social facilitation hypothesis of FC predicts that chimpanzees attend to FC as cues for new food-related learning opportunities. In line with this, we found that chimpanzees peered more toward the items in the FC condition (regardless of phase) and that this effect was modulated by conspecific presence. Specifically, peering was only significantly higher in the FC condition if conspecifics were not present. Considering that proximity was also higher in FC, this suggests that chimpanzees avoided peering at the items when others were around. If individuals did form expectations of the FC-associated items as being potentially edible, then this pattern of responses would seem to agree with what is known of food competition effects within chimpanzees' groups. Indeed, there is empirical evidence that competition is a stronger factor than dyadic tolerance or food quantity in feeding rates (Koomen & Herrmann, 2018), and chimpanzees are less likely to advertise food when quantities are small and/or indivisible (Hauser et al., 1993). Furthermore, chimpanzees are adept at following other individuals' gazes (Tomasello et al., 1998) and there is evidence that they can withhold such cues to prevent others from finding hidden foods, suggesting that

chimpanzees may understand that others can exploit their gaze (Hall et al., 2017). Thus, one possible explanation as to why peering occurred more in the FC condition only when conspecifics were absent is that they may have been using tactical deception to prevent competition over a potential food source (Hall et al., 2017). However, other explanations are possible, such as being distracted by other members, or even having learned the association between gazing and others locating the food without any cognitive inference. Given that we did not set out to test this, there is currently no way to disentangle these possibilities.

Furthermore, when freely able to interact with the two item types (Posttraining free interaction), chimpanzees consistently investigated the FC-associated item more than the GC-associated items, which is suggestive of the idea that FC signal a potential learning opportunity resulting in a bias of one's behaviors toward the associated item. Anecdotally, this was particularly striking in the juvenile's behaviors toward these items, as she repeatedly picked up and mouthed the FC-associated items while disregarding the GC-associated items after a single interaction. As there was only one juvenile in the group during the study time period, it is currently not possible to establish whether this is a general pattern. However, we know that mothers invest time and energy to help their young develop adaptive behaviors (Boesch, 1991; Hirata, 2009), that juveniles invest considerable amounts of time observing knowledge-able individuals (Biro et al., 2003; Biro et al., 2006; Boesch, 1991; Hirata & Celli, 2003) and that infant chimpanzees pay attention to their mothers' feeding behaviors (Ueno & Matsuzawa, 2005). Furthermore, there is evidence that food transfers in callitrichids are advertised by specific vocalizations (Rapaport & Brown, 2008; Roush & Snowdon, 2001). Thus, like in monkeys, mother chimpanzees may invest in their offspring's development by increasing their vocal input during foraging events. Indeed, callers would benefit from instilling knowledge in other naïve group members because this would increase the number of reliable signallers in the group and hence increase the caller's future foraging success. Mothers' inclusive fitness would also be increased if their infants quickly learned to discriminate palatable from noxious food and thus avoided making costly mistakes. To the best of our knowledge, there is no published account on the rate of food calling by females with and without infants, nor on the benefits young individuals can gain from having a knowledgeable individual that invests more time in producing facilitating signals. Yet, one could predict that mothers should call at higher rates (after controlling for other social and individual factors) if they are actively investing in their infants' development of foraging competencies and, within mother-young pairs, young naïve individuals of high-calling mothers may show increased beneficial outcomes such as faster mastery of food competencies and/or nutritional gains.

However, there was no evidence demonstrating that social food learning took place, as indeed we did not witness overt, clear-cut behavioral differences, such as more FC productions in the FC condition than the GC condition, a strong choice bias toward FC-associated items in the two-choice task or more mouthing of the FC-associated items than the GC-associated items during the free investigation period. This is in line with the idea that chimpanzee FC may not on their own trigger learning, unlike what can be seen in predator avoidance learning (Vieth et al., 1980), but rather that they can function as learning aids that prime individuals about a potential learning opportunity. In this view, the lack of overt differences could be explained by the fact that the vocalizations were not presented in conjunction with a feeding group member. Indeed, research shows that cross-modal integration may be required for stable and categorical learning (Leavens et al., 2010; Rowe, 1999; Savage-Rumbaugh, 1988). A multimodal playback experiment would further allow disentangling the role of FC in the social transmission process of food preferences, as it would allow contrasting their effects in the presence and absence of visual cues. However, it should be pointed out that the lack of preference in the forced choice task may also partly be due to the experimental setup. Indeed, the task was administered by the head keeper, who, as part of his daily work, often presents individuals with food and/or interesting items through the mesh (e.g., blankets and inedible play items). As such, the task may have been too similar to their daily interaction with the keeper, such that chimpanzees may not have had an incentive in making a specific choice, because of prior expectations of a positive outcome regardless of their choice. Presenting the two items simultaneously, without the familiar keeper being present, may have allowed us to better see if there truly was a preference for one item over the other. However, this was not feasible as individuals could not be separated to be individually presented with items left unattended.

There are a number of limitations that could not be avoided but should be acknowledged. Indeed, as we were unable to separate individuals, we had to test them as a group. Arguably, there was little that chimpanzees could learn from one another since until the very last day of the experiment, none were able to reach and interact with the items and as such could not serve as "demonstrators" that would promote social transmission (e.g., Hopper et al., 2011). Further, we found that conspecific presence did not influence proximity responses, yet there may be more subtle effects at play that we could not detect. For instance, socially bonded individuals tend to spend more time in close proximity (Mitani et al., 2000), such that some chimpanzees may have been remaining close to their social partners rather than intending to be close to the items. Thus while testing chimpanzees in groups is sometimes logistically/ethically unavoidable, and can sometimes provide more ecological relevance, it is important to be able to identify which social factors, such as social affiliation, genetic relatedness or dominance rank can influence the patterns found in the data. Unfortunately, it was beyond our ability to get more information on the social structure of this group of chimpanzees, as they have not been rigorously studied before. Another limitation is that we could only use vocalizations from one exemplar individual and were unable to test different kinds of items. We ensured that the vocalizations used were "typical" and originated from the same individual, such that potential individual idiosyncrasies may be expected to be similar across conditions. However, we do know for example, that FC vary according to food quality

(Slocombe & Zuberbühler, 2006), such that they could also have graded impacts on receivers' responses. The extent to which these variables influenced chimpanzees' responses cannot be assessed at this stage.

To conclude, our experiment contributes to an ongoing discussion, that is, why animals produce signals, such as food or alarm calls, that at first sight appear to disadvantage them in competing with others. As FC are consistently produced in the presence of food, they become reliable predictors of food to others, which increases competition. The main arguments put forward to explain this evolutionary conundrum are that callers could gain inclusive fitness benefits by informing kin members of the presence of food, or social benefits by declaring their foraging activity to others, including nonkin, either by becoming more predictable to others and thus avoiding unwarranted surprise encounters or by providing favors to others that enhances their social standing in the group. Our experimental data suggest a further possibility, that is, that individuals may reveal the presence of food as a vocal aid to promote learning of palatable items, which could benefit genetic relatives and ultimately lead to enhanced dietary diversity within social groups. However, while this study shows that receivers may be able to form expectations about novel objects based on conspecifics calls, whether senders aim at providing such information is currently unknown. Thus, further validation of the "social facilitating" hypothesis will be required and could include observational studies of wild females with and without infants, multimodal playback experiments, and importantly, replications of the study design in captive facilities that allow for individual separation.

AUTHOR CONTRIBUTIONS

Eloïse C. Déaux: Conceptualization (equal); formal analysis (lead); methodology (equal); supervision (equal); writing—original draft (equal); writing—review and editing (equal). **Clémence Bonneaud**: Conceptualization (equal); data curation (lead); investigation (lead); methodology (equal); writing—original draft (equal); writing—review and editing (equal). **Adrian Baumeyer**: Resources (equal); writing—review and editing (equal). **Klaus Zuberbühler**: Conceptualization (equal); funding acquisition (lead); methodology (equal); supervision (equal); writing—review and editing (equal).

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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