

Wild chimpanzees (*Pan troglodytes schweinfurthii*) distinguish between different scream types: evidence from a playback study

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Abstract When experiencing aggression from group members, chimpanzees commonly produce screams. These agonistic screams are graded signals and vary acoustically as a function of the severity of aggression the caller is facing. We conducted a series of field playback experiments with a community of wild chimpanzees in the Budongo Forest, Uganda, to determine whether individuals could meaningfully distinguish between screams given in different agonistic contexts. We compared six subjects' responses to screams given in response to severe and mild aggression. Subjects consistently discriminated between the two scream types. To address the possibility that the response differences were driven directly by the screams' peripheral acoustic features, rather than any attached social meaning, we also tested the subjects' responses to tantrum screams. These screams are given by individuals that experienced social frustration, but no physical threat, yet acoustically they are very similar to screams of victims of severe aggression. We found chimpanzees looked longer at severe victim screams than either mild victim screams or tantrum screams. Our results indicate that chimpanzees attend to the informational content of screams and are able to distinguish between different scream variants, which form part of a graded continuum.

Keywords Vocalisations · Playback experiment · Chimpanzees · Screams · Social cognition

Introduction

One particularly fruitful approach to studying animal communication has been to discriminate between signallers and receivers and to investigate their associated behavioural and cognitive processes separately (Seyfarth and Cheney 2003). As receivers, numerous mammalian species are capable of inferring different levels of information from conspecifics' vocalisations, including the relative size of the caller (Charlton et al. 2007), its identity (Rendall et al. 1996), the presumed affective state (Fichtel and Hammerschmidt 2003) and the context experienced by the caller (Seyfarth et al. 1980; for review see Zuberbühler 2003). Call comprehension by non-human primates is of particular interest for understanding the origins of language comprehension in humans. Much progress has been made in recent years on the meaning and function of social calls with various monkey species (e.g. Wittig et al. 2007a; Pfefferle et al. 2008), but there is a noticeable absence of evidence from great apes. Due to the phylogenetic proximity of great apes, such as chimpanzees, to our own species, they play a pivotal role in comparative approaches to understanding human language evolution (e.g. Tomasello 2008).

Two factors have contributed to the surprising lack of experimental evidence of call comprehension in any of the great apes. First, most great apes, including chimpanzees, have highly graded call systems that are difficult to examine. Second, for various ethical and logistical reasons, fieldworkers have generally avoided applying experimental techniques to wild apes, despite the advantages of playback

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experiments as tools in the investigation of call comprehension (Seyfarth et al. 1980). We are aware of only one playback experiment that tested call comprehension in apes and this was conducted with captive individuals (Slocombe and Zuberbühler 2005a). Two previous studies have used playbacks with wild communities, but in both cases the focus was on how chimpanzees responded to the presence of extra-community individuals (Wilson et al. 2001; Herbinger 2004).

In this study, we investigated call comprehension in wild chimpanzees, customising elements of the traditional playback paradigm, widely used with monkeys, for free-ranging chimpanzees. In particular, we examined patterns of social behaviour and aggression to ensure playbacks were not having a negative effect on the natural behaviour of the chimpanzees. The power of playback experiments is that they allow researchers to examine what information about ongoing events the animal can infer from simply hearing calls of others, in the absence of other contextual cues (Seyfarth et al. 1980). In the social domain, agonistic interactions are often accompanied by loud vocalisations and the ability to extract information about the nature of such events is advantageous for any social species, especially, if group members are not in constant visual contact with each other. Due to their fission–fusion society and the low visibility of their rain forest habitat, chimpanzees can normally only witness a small proportion of the daily agonistic events that take place in their community. The ability to understand the nature of such events and the identity of the group members involved would allow individuals to make a number of adaptive decisions, such as whether or not to intervene. In the wild, chimpanzees hear agonistic screaming bouts very regularly, suggesting that it would be extremely costly to respond to each call and thus natural selection should favour response selectivity. Intra-community aggression can escalate and can have fatal consequences (Townsend et al. 2007; Fawcett and Muhumuza 2000), and therefore it is vitally important for individuals to determine who is involved, how severe the conflict is likely to be, and whether support is needed. Second, the ability to monitor out-of-sight agonistic interactions will greatly increase the amount of social knowledge about third party relationships an individual can accumulate. Previous research has indicated that many primates, including chimpanzees, are very aware of third party relationships (Wittig et al. 2007b; Slocombe and Zuberbühler 2007) and in species where most interactions occur out of sight, some of this knowledge may be accrued through the auditory channel.

In most primate species, agonistic interactions are accompanied by scream vocalisations. Previous research has indicated that non-human primates can extract meaning from these calls. The agonistic screams of rhesus macaque

monkeys (*Macaca mulatta*) have been relatively well studied (Gouzoules et al. 1984, 1986). In this species, acoustic and behavioural analyses have indicated that the type of scream given by a caller depends on the severity of the attack and the rank of the opponent. Subsequent playbacks showed mother macaques were sensitive to this information conveyed in their offspring's screams, responding most strongly to screams that indicated a high risk of physical harm to her infant or a threat to the matrilineal dominance hierarchy (Gouzoules et al. 1984). Although there is evidence that screams carry fewer identity cues than other more tonal call types (Owren and Rendall 2003), Cheney and Seyfarth (1980) showed that vervet monkeys can make judgements about caller identity from screams; a finding replicated in rhesus macaques (Gouzoules et al. 1986; Fugate et al. 2008), Barbary macaques (Fischer 2004) and captive chimpanzees (Kojima et al. 2003).

Chimpanzees, such as macaque monkeys, produce screams in a context-specific manner. Although acoustically graded, screams given in different contexts vary consistently in some acoustic features. Individuals give acoustically distinct screams depending on their social role in a fight, with victims and aggressors producing distinct calls (Slocombe and Zuberbühler 2005b). We have also found a considerable degree of acoustic variation within the screams given by victims. These screams vary according to the severity of attack an individual is experiencing, with severe aggression (contact and directed chasing) eliciting screams that are higher in pitch, longer in duration and given in longer bouts than screams elicited by mild aggression (non-directed charging displays and postural threats) (Slocombe and Zuberbühler 2007).

In this study, we conducted a playback experiment with a habituated group of wild chimpanzees in the Budongo Forest, Uganda, to test if listeners could distinguish between victim screams elicited by different types of aggression. We predicted that if chimpanzees distinguished between different types of agonistic screams, they would show more interest to screams linked with significant social consequences, i.e., when the caller was experiencing severe aggression. In line with previous research (e.g. Cheney et al. 1995; Gouzoules et al. 1984; Pfefferle et al. 2008), we expected the chimpanzees to demonstrate this with a longer looking duration in the direction of the calls and a faster latency to orient towards them.

When comparing acoustically graded call types, such as chimpanzee screams, it is always possible to explain response differences as being driven directly by the acoustic features of the calls (Owren and Rendall 1997). For example, screams given to severe aggression could be more salient simply due to their longer duration and higher pitch compared to screams given to mild aggression. We

thus sought to investigate this hypothesis by presenting subjects with recordings of tantrum screams given by familiar infants experiencing extreme frustration, but no physical threat. Crucially, tantrum screams are acoustically more similar to the severe screams than mild screams. Therefore, if chimpanzees attend to the informational content of the screams (likely eliciting event, caller identity), we predict they should show the greatest reaction to severe victim screams and a weaker response to mild victim and tantrum screams. In contrast, if they respond to the most salient and intense acoustic signals in their environment, with no regard for the social meaning of these calls, we predict they should show the greatest reaction to tantrum and severe screams and a weaker response to mild screams.

Methods

Study site

The playback study was conducted with the members of the Sonso chimpanzee community (*Pan troglodytes schweinfurthii*) in the Budongo Forest, Uganda (Reynolds 2005). Budongo Forest covers an area of 428 km² of moist, semi-deciduous tropical rain forest, between 1°35' and 1°55'N and 31°08 and 31°42'E (Eggeling 1947). The community has been habituated since 1991 and has never been provisioned. During the period of study (January–November 2007), the group comprised 78 individuals, including 8 adult males, 25 adult females, 6 sub-adult males and 3 sub-adult females, all of which were individually identifiable, but with varying degrees of habituation.

Playback stimuli

Calls used as playback stimuli were recorded opportunistically from known individuals by KS using a Sennheiser ME66 microphone and a Sony TCD-D8 portable DAT recorder. Recordings of vocalizations were transferred digitally from the DAT recorder onto a PC (Toshiba, Celeron 1.8 GHz) at a sampling rate of 44.1 kHz, 16 bits precision, using Cool Edit Pro LE. Raven (Version 1.2) was used to cut the stimuli and to fade the background noise in and out at the start and end of each stimulus, to avoid the playback having an abrupt onset and offset. Stimuli contained only one chimpanzee calling and relatively low levels of background noise (cicadas, wind).

Playback stimuli consisted first of recordings of victim screams, originally given in response to severe and mild aggression. Each subject heard screams to both mild and severe aggression from the same individual. Mild and severe scream bouts were the same total length

(see Table 1) and contained three or four calls (mean calls/bout: severe = 3.83; mild = 3.86) that were given at approximately equal rates (mean calls/second: severe = 1.27; mild = 1.28). Each playback stimulus was approximately equal in total length (3 s) and we used Raven 1.2 to equate the stimuli in terms of root mean square (RMS) amplitude (see Table 1).

The victim screams were recorded from five sub-adult males (aged 12–16), who provided several exemplars of screams to both severe and mild aggression. We chose these individuals as they commonly attracted aggression from more dominant males, but they had not yet established any close relationships with group members apart from their mother and siblings. As responses of subjects were likely to have been influenced by their relationship with the caller, we ensured we paired subjects with a sub-adult male stimulus provider, to whom they were not directly related (not mother, father or maternal sibling) and where there was no evidence of a close relationship between the two in terms of either regular grooming or agonistic support (unpublished data).

Second, we tested subjects' responses to infant tantrum screams, which were comparable in their acoustic fine structure with the severe aggression screams (see Table 2). Since tantrum screams are rarely given by sub-adults, these screams were necessarily recorded from different individuals to the matched severe and mild victim screams each subject heard. Although this introduced a confound of identity, the tantrum screams still functioned as a valid test for whether chimpanzees merely attended to the peripheral acoustic features of our playback stimuli, rather than to the associated social information. Specifically, if their orienting response was merely driven by acoustic salience alone, then tantrum and severe screams should elicit stronger responses than screams given to mild aggression.

Chimpanzees of this community react to naturally occurring screams within about 30 m by orientating towards the sound source and occasionally by becoming pilo-erect, displaying or approaching. We did not want the chimpanzees to approach the speaker, as their suspicions

Table 1 The mean values and SD of the total stimulus duration and root mean square (RMS) amplitude for the stimuli in each condition

	Severe (N = 6)	Mild (N = 7)	Tantrum (N = 5)
Mean duration (s)	3.04 (0.20)	3.01 (0.11)	2.90 (0.21)
Mean RMS amplitude	8,423 (239)	8,367 (160)	8,433 (325)

RMS amplitude or 'effective amplitude' is equal to $\sqrt{\frac{\sum_{i=1}^n x_i^2}{n}}$, where n is the number of samples in the selection and x_i is the amplitude (in dimensionless sample units) of the i th sample in the selection. *Units* dimensionless sample units

Table 2 The mean values and SD of four acoustic measures for each scream condition

	1st formant (Hz)	SD	Peak freq of fundamental (Hz)	SD	Duration (s)	SD	Mean pitch (Hz)	SD
Tantrum ($N = 5$)	1,451	92.8	1,574	103.9	0.44	0.1	1,450	113
Severe ($N = 6$)	1,435	38.4	1,436	62	0.54	0.17	1,404	58.6
Mild ($N = 7$)	1,261	201	1,276	189.3	0.31	0.15	1,064	215
Mann–Whitney U value	12 ($P = 0.662$)		4 ($P = 0.052$)		10 ($P = 0.429$)		10 ($P = 0.429$)	

N refers to the number of scream bouts (used as stimuli) that contributed to the mean values reported in each category. Mann–Whitney U tests were conducted to test for differences between the acoustic structure of severe victim ($N = 6$) and tantrum screams ($N = 5$) only

would have been aroused upon finding no chimpanzee at the corresponding location. Such an experience may have disturbed the chimpanzees and may have altered their responses to future playbacks. We therefore limited the playback stimuli to a short bout of screaming of approximately 3 s. Pilot observations indicated this duration was long enough to elicit interest in the stimulus without inciting approach.

Acoustic analysis of stimuli

We measured each call in each scream bout stimulus along the following four parameters: (1) duration (s); (2) mean frequency of the fundamental frequency (Hz); (3) mean frequency of the first formant (Hz); (4) peak frequency in the fundamental (Hz). These measurements were conducted using Praat version 4.3.37. We created spectral slices to measure peak frequency and measures of mean frequencies of the fundamental and first formant were conducted using scripts written by M. Owren (unpublished data). For each acoustic parameter, we then calculated a median value for each scream bout (consisting of 3–5 calls). Subsequently, we averaged the values for the scream bouts in each stimulus class to illustrate the differences and similarities between the stimulus classes (severe, mild and tantrum; see Table 2). These analyses were first able to confirm the pattern of acoustic differences between mild and severe victim screams, as reported by Slocombe and Zuberbühler (2007). Second, the measurements of severe victim screams and tantrum screams were very similar, with no acoustic measurement showing a significant difference between the two types of calls. Thus, in terms of the key acoustic variables that distinguish severe from mild victim screams, severe victim and tantrum screams are very similar.

Protocol

The protocol follows the same principles as traditional playback experiments conducted with monkey species (Seyfarth et al. 1980), but had some additional features to maximise the

suitability of this paradigm for this fission–fusion great ape species. The study consisted of severe scream, mild scream, and tantrum scream trials that followed a within-subject design. To avoid order effects, we counterbalanced trials, ensuring subjects did not hear conditions in the same order. We waited at least 1 day in between trials and the same focal subject never appeared in consecutive experiments. Playbacks occurred between 8 a.m. and 4 p.m., typically at around 11 a.m. ($\text{mean}_{\text{time of day}} \pm \text{SD} = 11.08 \pm 2.12$ h). Screams can occur naturally at a high daily rate (approximately 6 scream bouts per hour) in this chimpanzee community (Slocombe and Townsend, unpublished data), however, playbacks were conducted at a very low rate over 10 months ($\text{mean} = 3$ per month, $\text{range} = 0\text{--}7$ per month). We also ensured that no chimpanzee heard the same stimulus twice. If a subject had been in the vicinity of a playback we conducted with another focal, we played a different exemplar to that individual, rather than repeat the same stimulus he or she may have overheard.

Before conducting any trials, we checked that all stimuli sounded natural to an experienced human listener at a distance of 30 m and could not be heard clearly behind the speaker at 100 m. Stimuli were stored and played in WAV format on an APPLE Ipod Nano and broadcast using a NAGRA DSM speaker/amplifier. The speaker was concealed in a modified rucksack (hole cut into the fabric where the sound was emitted to ensure an undistorted broadcast) throughout the experimental period so the chimpanzees never saw the equipment in operation.

A minimum of three operators were required to run the experiment in a fashion that maximised the realism of the playbacks: operator 1 (O1), to stay with the experimental subject, the receiver of the vocalisation (always ST or KS); operator 2 (O2), to stay with the ‘scream provider’ (the individual whose calls we played from the speaker); operator 3 (O3), to play the stimulus from the speaker. We used Motorola GP340 radios or Nokia 2600 mobile phones to maintain contact between all the three operators throughout the duration of the experiment. Each operator collected data on a number of behaviours prior to and following a playback.

1. O1 followed the experimental subject for an average of 188 min (± 131 SD) before playbacks, and after playbacks they continued to follow subjects for a mean duration of 69 min (± 30 SD). O1 recorded all occurrences of aggression, specifically, the number of aggression bouts involving adults, sub-adults or juveniles that occurred in the subject's party. Bouts including contact, directed or non-directed aggression (Slocombe and Zuberbühler 2007) were considered. In addition, the duration and number of all screaming bouts the subject heard were also recorded (type of scream not ascertained as most occurred out of sight). All observations of grooming and pant-grunting (a social greeting vocalisation given by subordinates to dominants) received and given by the subject were also recorded. Once a playback was completed, O1 noted the identity of all individuals in the party to ensure that future playback subjects would not receive a stimulus they may have previously overheard.
2. O2 recorded the time and nature of all loud vocalisations made by members of the scream provider's party and the identity of the vocalising individual. This allowed us to ensure the scream provider had not announced his true location in the forest just before playback. In addition, the general behaviour of the scream provider (e.g. grooming, resting, feeding) and the time at which it changed were also recorded. O2 particularly looked for behavioural changes at the time of the playback, however, the scream provider was never observed to show any orientation or approach to the speaker or a change in broad behavioural category (rest, travel, feeding) at the time of playback.
3. O3 positioned and operated the playback equipment, whilst keeping a record of all group members that were within a 50 m radius of the speaker at the time of the playback.

To prevent the scream provider from hearing his own vocalisation, he had to be >100 m away from the speaker (see Fig. 1). The mean distance of the scream provider to the speaker was 355 m (± 262 SD).

As soon as the experimental subject was resting on the ground (without feeding or grooming, which may distract him from the stimulus or to make his response ambiguous) and alone (to exclude the possibility that any subsequent response to the stimulus was a result of social referencing), the operator 3 took the loudspeaker 30 m away from the subject in the direction of the scream provider and concealed himself. In order to prevent unwillingly exposing any chimpanzee to an intense stimulus we ensured no other chimpanzees were within 30 m of the speaker before the screams were played back. In the absence of the scream provider's vocalisations, this experimental set-up realistically

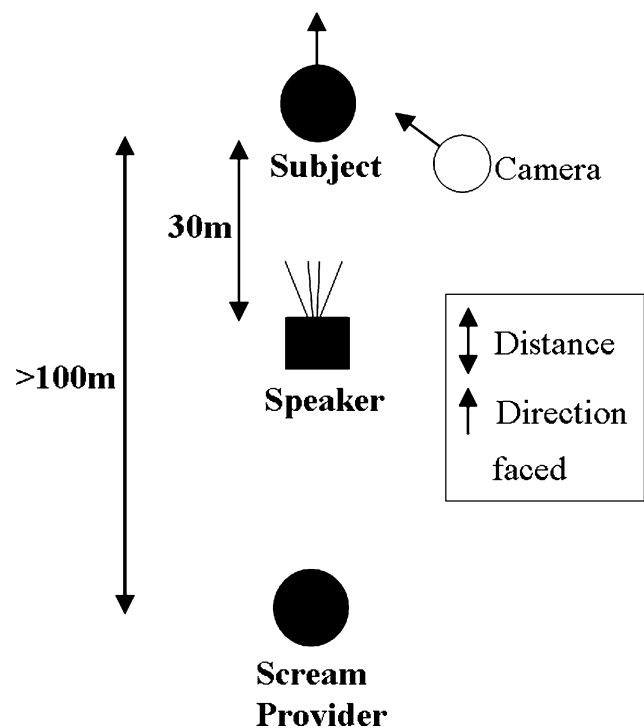


Fig. 1 Schematic representation of experimental set-up

simulated the presence of another chimpanzee 30 m away, involved in either an agonistic interaction of severe or mild intensity or a tantrum.

Another prerequisite was that the subject had to be facing away from the speaker so any orientation response was unambiguous. When this condition was met, operator 1 used a Panasonic NV-GS 250 digital video camera to film the subject for 30 s before and 1 min after playback. Due to the low visibility at this site, operator 1 usually had to be within 10 m of the subject and only the very well-habituated individuals of this community would tolerate this, when alone on the ground. Operator 1 was responsible for checking with the other operators that all conditions had been met before telling the operator 3 to play the stimulus.

Playback trials and data analysis

A total of six well-habituated subjects were tested in all the three conditions, four adult females and two adult males. Five of the six were tested only once for each condition. However, one female subject heard severe and mild stimuli from two different individuals (severe $N = 2$; mild $N = 2$) and showed the same pattern of response to both sets of stimuli. To avoid pseudo-replication, we averaged her responses for each of the two conditions. Two further females only received the tantrum scream condition and thus could not be included in the final analyses. However, their responses to this condition were very similar to the

responses of the other six subjects tested in that they were slow to orient to the speaker and looked only once towards it for a short period of time (duration of looking to speaker = 0.68 s; 3.2 s).

Videotapes were coded frame by frame using Adobe Premier Pro CS3 software. The following three behavioural responses were measured: (1) *latency* time from stimulus onset to the subject orientating its head towards the speaker. In one tantrum trial, the subject did not orient to the speaker at all. We thus allocated her a “ceiling latency”, which was the maximum latency observed from the analysed trials to allow her inclusion in latency analyses. (2) *Looking duration* time for which the subject oriented its head towards the speaker in the minute after the onset of the playback. (3) *Number of looks* number of looks towards the speaker in the minute after the onset of the playback.

To ensure accurate coding of videotapes, a second coder, blind to the trial type, was asked to analyse 25% of trials (5 trials). We compared the measures taken by each coder and found very high levels of agreement [Pearson’s correlation ($N = 5$) for latency = 0.97; duration 0.93; number of looks = 1.00].

Statistical analysis

Parametric and non-parametric tests were used for comparisons (SPSS version 12.0). All tests were two tailed. In cases where we were dealing with small sample sizes, we conducted non-parametric tests and we calculated exact P values, as opposed to asymptotic ones, as recommended by Mundry and Fischer (1998).

Results

Behavioural responses

Severe versus mild screams

We predicted that if subjects processed the information conveyed by screams, they should respond more strongly

to severe than mild screams. Our prediction was supported: during the minute following playback subjects looked towards the speaker for longer in response to severe than mild screams (exact Wilcoxon matched-pairs signed-rank test: $Z = -2.20$, $N = 6$, $P = 0.031$; see Table 3; Fig. 2). They also looked more times to severe screams, but this was not significant ($Z = -2.06$, $N = 6$, $P = 0.06$; see Table 3). Lastly, although they looked more quickly towards severe screams, this also did not reach significance ($Z = -1.57$, $N = 6$, $P = 0.156$). Despite the last two measures yielding insignificant results, estimates of effect size (see Table 3) indicate that the effect size remained large across all the three measures.

Severe screams versus tantrum screams

If subjects’ responses to severe screams were being driven purely by the saliency of the sound, we would expect subjects to show roughly equal interest in both the severe and tantrum screams, as they are similar in acoustic structure. In contrast to this prediction, subjects looked towards the speaker for longer (exact Wilcoxon matched-pairs

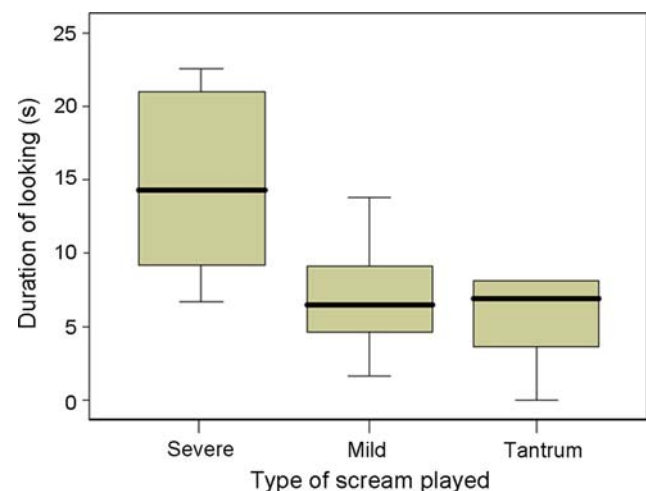


Fig. 2 Boxplots illustrating the total duration spent looking at the speaker in the minute after playback in response to three types of playback stimuli. Boxplots illustrate medians, interquartile ranges and highest and lowest values

Table 3 Behavioural responses of subjects to each of the three playback conditions

	Severe ($n = 6$)	Mild ($n = 6$)	Tantrum ($n = 6$)	Cohen’s d	
				Severe vs. mild	Severe vs. tantrum
Mean latency (s)	1.19 (0.35)	1.72 (0.72)	2.64 (0.91)	1.00	1.05
Mean duration of looking (s)	14.66 (6.87)	6.99 (4.12)	6.79 (5.11)	1.37	1.31
Mean number of looks	2.58 (1.20)	1.16 (0.41)	1 (0.63)	1.76	1.73

Mean values across the six subjects and the standard deviations are shown. Estimates of effect sizes for the differences between severe and mild conditions and severe and tantrum conditions are illustrated by Cohen’s d values

signed-rank test: $Z = -2.23$, $N = 6$, $P = 0.031$; see Table 3; Fig. 2), more times ($Z = -2.20$, $N = 6$, $P = 0.031$; see Table 3) and more quickly ($Z = -2.20$, $N = 6$, $P = 0.031$; see Table 3) in response to severe compared to tantrum screams. The effect sizes associated with the comparison of these conditions across all three measures were large (see Table 3).

Effect of prior exposure to screams

Our results are consistent with the idea that chimpanzees process the social information contained within screams and are not just responding to the acoustic intensity of the signal. However, as screaming also occurred naturally during the study period, a subject's responses could have been modulated by these events.

In order to examine the effect of prior exposure to naturally occurring screams, we calculated the number of screaming bouts the focal subjects saw or heard in the hours we followed them before a playback trial occurred. Mean duration of screaming exposure did not differ significantly between conditions (severe vs. mild: independent t test, $t = 0.219$, $N_{\text{severe}} = 7$, $N_{\text{mild}} = 7$, $P = 0.831$; severe vs. tantrum: independent t test, $t = -0.741$, $N_{\text{severe}} = 7$, $N_{\text{tantrum}} = 6$, $P = 0.474$).

Behavioural changes in response to playback experiments

Our experiments raise some ethical concerns. For example, the possibility exists that simulating agonistic encounters with playbacks increase subsequent levels of aggression in the community. To investigate this possibility, we performed three additional post hoc analyses.

Immediate aggression

First, we investigated whether our playbacks caused any immediate effects by analysing levels of aggression in the hour preceding and following playbacks. We used duration of screaming and number of screaming bouts heard as an indirect measure of aggression. We predicted that if playbacks intensified levels of aggression, then more screaming should be heard in the hour following experiments. We found no evidence to support this prediction. In fact, it seemed more screaming occurred in the hour before playback compared to the hour after, although this was not significant (mean scream duration_{hour before} = 46.7 s, SD = 61.7; mean scream duration_{hour after} = 18.8 s, SD = 29.5; paired sample t test: $t_{(20)} = 1.97$, $P = 0.06$; mean number of scream bouts_{hour before} = 2.95, SD = 2.7; mean number of scream bouts_{hour after} = 1.7, SD = 2.0; paired sample t test: $t_{(20)} = 1.724$, $P = 0.10$).

Second, because aggression levels vary throughout the day, with less fighting generally occurring in the heat of the day, we also analysed exactly the same time periods on 'matching control' days when conditions for playback were not met and therefore no playback occurred. We found a similar pattern of less screaming and therefore less aggression later in the day on non-playback days, but again this was not significant with either measure of screaming (mean scream duration_{hour before} \pm SD = 70.8 \pm 112.0 s; mean scream duration_{hour after} \pm SD = 44.7 \pm 66.4 s; paired sample t test: $t_{(20)} = 1.73$, $P = 0.09$; mean scream bouts_{hour before} \pm SD = 4.4 \pm 5.6; mean scream bouts_{hour after} \pm SD = 2.9 \pm 3.9; paired sample t test: $t_{(20)} = 1.887$, $P = 0.075$).

It is apparent that there was generally less aggression, as measured in terms of screaming, on days when we performed a playback experiment. This was probably because it was more difficult to meet all conditions necessary to perform a playback on days when aggression levels were high, but the daily pattern of aggression was stable across days with and without playbacks. Taken together, these results indicate that playbacks had no immediate effects on the daily pattern of aggressive incidents in this community.

Long-term aggression

In a third analysis, we looked for long-term effects by comparing direct measures of aggression levels across years. Of the 20 playbacks considered, 7 occurred within 1 month (January 2007) when conditions were optimal. We compared all occurrences of aggressive interactions that took place in January 2007 and compared them with the matched period in the previous year (Slocombe, unpublished data). In January 2006, there were on average 0.97 aggression bouts per hour (48 bouts observed over 49 h focal time) and in January 2007, there were on average 0.93 aggression bouts per hour (73 bouts observed over 79 h). We concluded that scream playbacks did not adversely affect the general levels of aggression in the Sonso community.

Other social behaviour

To see if other social behaviours were affected by playbacks, we recorded grooming and pant-grunt vocalisations prior to and after playbacks. However, because we aimed to undertake playbacks when individuals were alone, social interactions were consequently limited. In fact, grooming and pant-grunting were only seen to occur once before a playback and twice following a playback. We therefore could not conduct any meaningful analyses with regards to changes in social behaviours, but our impression was that

playbacks did not appear to influence the usage of these behaviours.

Discussion

Using playback techniques, we found that chimpanzees show more interest in screams given during severe rather than mild aggression. When listening to a short bout of screaming from an unrelated individual in response to severe aggression, subjects looked at the speaker for longer than when they heard the same individual's screams given to a case of mild aggression. Although with our small sample size we were unable to detect significant differences in latency to orient to the speaker and number of looks to the speaker between these two conditions, these measures also varied in the expected direction and the effect sizes remained large. This firstly shows that chimpanzees are capable of distinguishing between these calls despite their highly graded nature, an ability well documented in other primates (e.g. Fischer 1998), including humans (e.g. Liberman et al. 1957). Graded call systems, like that of the chimpanzee, can convey a number of discretely perceived call variants. This greatly increases the potential size of the vocal repertoire and thus the potential complexity of the vocal system.

Our results are also consistent with the notion of subjects extracting information about the severity of the attack from the scream and that they processed call meaning rather than had their responses driven solely by the acoustic features of the stimulus presented to them. Whilst tantrum screams matched severe victim screams in a number of key acoustic features, individuals showed little interest in this call type, showing they were not simply orienting to the most acoustically salient sounds. Chimpanzees looked at the speaker more slowly for less time and less often to tantrum compared to severe screams. This result confirms informal observations that tantrum screams are largely ignored by unrelated community members and indicates that chimpanzees are thus attending to the informational content of calls (identity of caller, likely eliciting event). As tantrum screams were given by a different individual to the matched victim screams, these results need to be viewed tentatively. Nevertheless, this comparison indicates that chimpanzees do not just orient to the acoustically most salient stimuli in their environment, and therefore the difference in responses to severe and mild victim screams seems unlikely to be merely because the severe screams are acoustically more salient.

Our study is consistent with the idea that chimpanzees can infer the severity of an attack from listening to the screams alone. This supports the notion that chimpanzees understand interactions they are unable to see. It also

highlights the wider implication that information gathered through the auditory modality about distant events may have a greater influence on wild chimpanzee behaviour than previously recognised.

The listeners' reasons for showing more interest in a severe rather than a mild attack remain obscure at this stage. Listeners may be deciding whether to intervene and therefore trying to judge how much the victim needs their support. Alternatively, given the well-documented 'selfish' nature of chimpanzees (Silk et al. 2005), the subjects may be responding to maximise their own safety. An individual resting on the ground is potentially vulnerable to attack and evasive action may be needed. The potential risk to the listener can be extrapolated from the type of aggression being experienced by the caller and therefore it makes sense for resting individuals to attend more to events that may signal greater danger for them.

The majority of work done on chimpanzee cognition is currently performed in captivity. Despite all the progress in recent years, captive studies generally suffer from low levels of ecological validity. Field playbacks using social signals have led to great advances in our understanding of social cognition in other primate species (e.g. Cheney and Seyfarth 2007; Bergman et al. 2003) and the customised protocol outlined here may have the potential to foster further research on chimpanzee vocal communication and social cognition. This study has shown that field playback experiments are possible with apes, just as they are with monkeys. Although the number of protocol prerequisites is onerous, with a correspondingly slow rate of data collection, they are essential to generate a realistic scenario. As with all playback experiments, this is critical to obtain meaningful results and minimise the chances of disturbing the animals by presenting them with implausible or impossible events. For ethical reasons, we consider it essential that measures of aggression and other social behaviours continue to be collected ensuring that these field experiments do not negatively impact on the natural behaviour of these endangered animals.

To conclude, our study has demonstrated that intra-group playback experiments using social signals can be successfully conducted with wild chimpanzees. We found that individuals distinguish between different types of screams, which form part of a larger graded call system. They also extract the corresponding social information from the screams they hear, consistent with the notion chimpanzees process the meaning of the call rather than just responding to salient acoustic features.

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