



Vocal, gestural and locomotor responses of wild chimpanzees to familiar and unfamiliar intruders: a playback study

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Wild chimpanzees can be dangerously violent against individuals that do not belong to their community, indicating a strong selection pressure on decision-making abilities in this context. The presence of a neighbouring male indicates a serious threat, although encountering an unfamiliar male is potentially even more dangerous because it indicates the arrival of a new group with whom the subjects have no previous history of interaction. We conducted playback experiments with members of three chimpanzee, *Pan troglodytes verus*, communities in the Taï National Park, Côte d'Ivoire, in which we simulated the unexpected presence of another chimpanzee. We tested subjects' responses to pant hoots of familiar group members, neighbouring individuals and unfamiliar strangers. We found that neighbours and strangers elicited a wider range of gestural signals than familiar group members. Vocal responses were common in all conditions. Familiar group members mainly triggered pant hoot replies, whereas neighbour and stranger trials caused screams. Across conditions, males responded more strongly than females. Male party size had an effect on subjects' vocal responses to strangers but not to neighbours, although neighbours were approached more closely. Our results show that chimpanzees are able to identify different classes of individuals by their pant hoot vocalizations, as judged by their differential responses to the calls of familiar group members, neighbours or strangers. The overall response patterns suggest that chimpanzees are aware of the different social consequences associated with encountering a neighbouring group or a group of strangers.

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An important aspect of social behaviour in territorial animals concerns the relationships that individuals maintain with their neighbours. In most social species, the topic has received relatively little empirical attention, especially if compared with the amount of work devoted to understanding intragroup social behaviour. A consistent finding in research on intergroup relations has been that many species can discriminate neighbours from strangers, with the latter generally eliciting more aggressive behaviour (e.g. Temeles 1994; Muller & Manser 2007). There is also good evidence for vocal recognition of neighbours, especially in birds (e.g. McComb et al. 1993; Lambrechts & Dhondt 1995; Lovell & Lein 2005). However, most studies have been conducted with species where the group size and number of neighbours are small and stable over time (Falls

1982; Lambrechts & Dhondt 1995; Stoddard 1996). Apart from some exceptions, the evidence for vocal recognition of neighbours is particularly weak in nonhuman primates (Cheney & Seyfarth 1982; Wich et al. 2002, 2004). For chimpanzees, *Pan troglodytes*, it is not known whether individuals are able to recognize out-group members individually. Intergroup interactions occur relatively frequently and vocal recognition is likely to play a crucial role because of the very limited visibility in their natural habitat.

Long-term studies have found that free-ranging chimpanzees can respond very aggressively to individuals that are not members of their own community (Kawanaka & Nishida 1974; Goodall 1986; Boesch & Boesch-Achermann 2000; Wilson & Wrangham 2003; Wilson et al. 2004; Mitani and Watts, 2005; Muller & Mitani 2005; Watts et al. 2006; Boesch et al. 2008). This is particularly true when adult males encounter neighbouring males, although females sometimes participate in intergroup interactions as well, usually by vocalizing and sometimes approaching (Boesch & Boesch-Achermann 2000; Boesch et al. 2008). Although not every intergroup interaction leads to overt aggression, chimpanzees are prepared to inflict physical harm to out-group individuals, which can lead to severe injury and death (see Manson & Wrangham 1991; Muller 2002; Boesch et al. 2008).

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A more common form of intergroup interaction in chimpanzees is by means of auditory signals (Boesch et al. 2008). Typical vocalizations used during intergroup interactions are pant hoots and screams. Pant hoots carry over considerable distances, even through dense forest habitat, and are often reciprocated, thereby revealing the callers' whereabouts to other group members and neighbours in the vicinity (Boesch & Boesch-Achermann 2000; Wilson et al. 2001). These calls are mainly produced by adult males, usually in the vicinity of others (Crockford & Boesch 2003; Notman & Rendall 2005). Acoustically, pant hoots are individually distinct but there is also evidence that group members within a community converge on community-specific call variants (Marshall et al. 1999; Mitani et al. 1999; Crockford et al. 2004), although it is not clear whether any of these acoustic features are meaningful to receivers. The other call type, commonly produced during intergroup interactions, is the scream. Screams do not propagate very far and thus function to communicate to nearby individuals of the same travel party. Previous work has shown that screams are acoustically highly variable, and some variants serve as reliable indicators of the social role and ongoing context that the caller is engaged with (Zuberbühler 2000; Slocombe & Zuberbühler 2005, 2007; Slocombe et al. 2009).

In terms of nonvocal behaviour, a typical behavioural strategy in the intergroup context is patrolling (Boesch & Boesch-Achermann 2000; Mitani & Watts 2005). Here, individuals travel silently and carefully with raised hair, usually in a single file, and in close proximity to one another. They rarely feed but stop occasionally to scan or sniff. The travel direction of a patrol is typically aimed towards the edge of the territory, sometimes trespassing into the neighbouring group's territory. Males appear to initiate border patrols only when party size is above a certain threshold (Boesch & Boesch-Achermann 2000) and, if neighbours are encountered, a frequent observation is that individuals either retreat or that they initiate auditory or physical contact. In the latter case, displays sometimes precede chasing, hitting, holding down or biting an opponent. The most detailed descriptions of violent encounters between chimpanzee communities have been reported at the Gombe and Ngogo study sites (e.g. Goodall et al. 1979; Goodall 1986; Mitani and Watts 2005; Watts et al. 2006). If violence erupts, victims can sustain severe injuries within minutes, although aggressors sometimes also get hurt (Manson & Wrangham 1991; Boesch & Boesch-Achermann 2000; Williams et al. 2004). Rapid support from other group members is crucial during such events, and victims often manage to escape when other group members arrive (Boesch & Boesch-Achermann 2000; Boesch et al. 2008).

With this study, we sought to examine the role of vocal signals in the causation of intergroup behaviour in wild chimpanzees. We were especially interested in whether chimpanzees recognized the pant hoots of individuals belonging to their own group, a neighbouring group or an unfamiliar group. Intergroup interactions are difficult to study systematically in the field because they are not very common and typically involve individuals that are not habituated to the presence of human observers. In the Sonso community of Budongo Forest, Uganda, for example, an intergroup interaction may have been terminated by the presence of human observers (Reynolds 2005). To understand the causal role of vocalizations and to investigate chimpanzees' responses to the presence of other individuals more systematically, we conducted a playback study with three chimpanzee communities in the Tai National Park, Côte d'Ivoire. Individuals were presented with recordings of pant hoot vocalizations of familiar group members, neighbouring individuals or unfamiliar strangers. We were interested in the subjects' overall response profiles to the three conditions, and in the contributions of different group members.

METHODS

Study Site and Individuals

We studied three habituated communities of free-ranging chimpanzees, *P. t. verus*, in the Tai National Park, Côte d'Ivoire (5°52'N, 7°20'E), which inhabit a largely intact area of tropical forest of about 200 km² combined (Boesch et al. 2008). The three communities have been habituated to human observers for several years (first continuous follows of habituated individuals: group N: 1982; group S: 1993; group M: 1995). Key demographic data are summarized in Table 1. Calls used for playback stimuli were recorded between January and June 1999. Playback experiments were conducted between July 1999 and June 2001 (Herbinger 2004). See the Appendix for ethical issues arising from the playbacks. The research was approved by the Max Planck Society, the 'Ministère de l'Enseignement Supérieur et de la Recherche Scientifique' and the 'Ministère de l'Environnement, des Eaux et Forêts, Côte d'Ivoire.

Playback Experiments

The playback experiments were designed to investigate systematically the behaviour of wild chimpanzees on the sudden and unexpected appearance of another individual in the vicinity. Methodologically, the study built on earlier work conducted with birds (Brooks & Falls 1975) and monkeys (Cheney & Seyfarth 1982). We used pant hoot vocalizations to simulate this social event, both because there are good indications that these calls are individually distinctive and because they travel well over long distances (Mitani et al. 1996; Boesch & Boesch-Achermann 2000; Kojima et al. 2003). Playback stimuli consisted of recordings of 46 chimpanzee pant hoots, obtained from 14 adult males. No stimulus was played to a community more than once. Calls were recorded with a Marantz-PMD 222 portable cassette recorder and a Sennheiser ME66/K6 directional microphone, subsequently digitized with Canary 1.2.4 (sampling frequency 22.05 or 44.1 kHz/16 bits; Cornell Laboratory of Ornithology, Ithaca, NY, U.S.A.). In each trial, we played back a recording of a single pant hoot from a distant speaker to a party of chimpanzees, which served as the focal unit. Stimuli were selected so that they simulated one of the following conditions: (1) 'member': a pant hoot originally recorded from one of eight different males of the same community; (2) 'neighbour': a pant hoot recorded from one of eight males of a neighbouring community; (3) 'stranger': a pant hoot recorded from one of six males of the Guiroutou community, approximately 70 km to the south, which the subjects had never met. We were particularly interested in whether chimpanzees discriminated between the calls of neighbours and unfamiliar strangers, how they responded to them, and whether they took into account the current social conditions.

Table 1
Composition of the three communities at the time of the study (July 1999)

Age/sex class	Community		
	North	Middle	South
Adults ♂/♀	2/7	3/3	3*/20
Adolescents ♂/♀	0/1	0/1	1/0
Juveniles ♂/♀	2/5	0/1	10/1
Infants ♂/♀	3/3	1/1	11/5
Total	23	10	51

* One male died of old age in August 1999.

We took great care to present the stimuli in a spatially realistic way. We conducted all trials in the peripheral zone of the focal party's territory, beyond the core area that was used 75% of time (Herbinger et al. 2001). We conducted all 'neighbour' trials in the overlap zone of the two territories and from the appropriate direction. For 'member' trials, we ensured that the individual whose calls we played back had not been seen or heard in the previous hour. For each trial, a field assistant moved approximately 350 m (range 200–600 m) from the focal party towards the territory border, while maintaining radio contact with the experimenter (I.H.).

We conducted playback experiments at a very slow rate, matching the natural occurrence of intergroup encounters. Neighbour and stranger trials were separated by a median interval of 16 days, which is comparable to the range of natural intergroup encounters in Tai (directly observed encounter rate: 0.8–1.6 per month; estimated true encounter rate: 1.6–3.2 per month; Boesch & Boesch-Achermann 2000; Boesch et al. 2008).

Calls were broadcast with a Pyle-SA 3000 cassette player connected to a customized 200 W K+H ELA-RW 120 speaker-amplifier. The amplitude was adjusted so that the mean peak sound pressure level was at 103.4 ± 1.1 dB, measured at 1 m, for all stimuli to ensure that response differences could not be explained by mere amplitude differences. The sound pressure level was chosen so that it matched that of naturally produced pant hoots. If the pant hoots were not audible to the experimenter staying with the focal party the trial was discarded ($N = 5$ cases). Immediately after each playback trial, the field assistant removed the playback equipment and moved away to prevent the chimpanzees detecting the true cause of the disruption.

DATA ANALYSIS

We recorded all vocal responses and all accompanying behaviours of party members on an all-occurrence basis for a period of 2 h following each playback trial. Pilot data indicated that this time period was sufficient to cover the focal animals' maximum changes in their spatial location to the playback stimuli, hence including an important long-term effect. Data were collected with a Psion Organiser hand-held computer and Observer software (Noldus Information Technology, Wageningen, The Netherlands). Vocal responses were recorded with a Sony Professional WM D6C portable cassette recorder and a Sennheiser ME66/K6 directional microphone, with additional oral comments given if behaviours changed rapidly. We used PRAAT (www.praat.org) to inspect the vocal responses and conducted basic analyses of responses at different time intervals: 20, 60 and 120 min after a playback trial. Statistical analyses were conducted with SPSS 12 (SPSS Inc., Chicago, IL, U.S.A.). All tests were two tailed.

RESULTS

Vocal Responses

Subjects produced a number of behavioural and vocal responses when hearing another male's pant hoot vocalizations. The most common vocal responses to pant hoots of another chimpanzee were screams and pant hoots, but the experimental condition had a significant effect on call type. The most common response to a group member was a pant hoot reply (72.7% of trials), which was significantly different from responses to strangers or neighbours (0.0% and 4.5%, respectively; overall chi-square: $\chi^2_2 = 30.752$, $P_{\text{exact}} < 0.001$; chi-square tests between conditions: member versus stranger and member versus neighbour, two-tailed: $\chi^2_1 = 19.605$; $\chi^2_1 = 17.188$; both $P_{\text{exact}} < 0.001$; neighbour versus

stranger: $\chi^2_1 = 0.931$; $P_{\text{exact}} > 0.3$). There was a nonsignificant trend towards more screaming in response to neighbours than group members, but not between strangers and group members (overall chi-square: $\chi^2_2 = 6.176$, $P_{\text{exact}} = 0.053$; chi-square between conditions: member versus neighbour: $\chi^2_1 = 7.222$, $P_{\text{exact}} = 0.013$; member versus stranger: $\chi^2_1 = 0.888$, $P_{\text{exact}} = 0.465$; neighbour versus stranger: $\chi^2_1 = 3.815$, $P_{\text{exact}} = 0.069$). Latency to screaming was also affected by the experimental condition (Kruskal–Wallis one-way analysis of variance by ranks: $H_2 = 5.655$, $P = 0.059$). Latency measures were shorter for neighbours ($N = 22$) than group members ($N = 11$) while more screaming bouts occurred during the first 5 min (Mann–Whitney U tests, two-tailed: latency: $Z = -2.677$, $P_{\text{exact}} = 0.006$; N screaming bouts: $Z = -2.197$, $P_{\text{exact}} = 0.026$). No significant differences were found between strangers and group members. Other vocal responses, as well as drumming behaviour, were infrequent and sample sizes generally too small to conduct meaningful statistical comparisons. The signalling responses in the three playback conditions are summarized in Table 2.

Gestures

In terms of gestural signals, hunching, grinning and mounting/embracing were most common but there were no significant differences overall (overall chi-square: hunching: $\chi^2_2 = 4.070$, $P_{\text{exact}} = 0.145$; grinning: $\chi^2_2 = 5.810$, $P_{\text{exact}} = 0.590$; mounting/embracing: $\chi^2_2 = 2.349$, $P_{\text{exact}} = 0.308$). When we compared the overall rates of the four gestures combined between the three conditions there was no significant effect (Kruskal–Wallis one-way analysis of variance by ranks: $H = 5.33$, $P = 0.07$); there was a significant difference between member and neighbour (Mann–Whitney U test: $U = 62.5$, $Z = -2.257$, $N_1 = 11$, $N_2 = 22$, $P_{\text{exact}} = 0.024$), but not between member and stranger (Mann–Whitney U test: $U = 70.0$, $Z = -6.664$, $N_1 = 11$, $N_2 = 20$, $P_{\text{exact}} = 0.104$) or neighbour and stranger (Mann–Whitney U test: $U = 188.5$, $Z = -0.798$, $N_1 = 22$, $N_2 = 20$, $P_{\text{exact}} > 0.3$). Other gestures were less common but it is possible that some of them, such as touching or putting a finger into someone's mouth, were the product of the same underlying motivation (Table 2).

Table 2

Relative frequency of different communication behaviours of subjects given to the simulated presence of another chimpanzee within the first 5 min (N trials)

Behaviour	Playback condition		
	Member ($N=11$)	Neighbour ($N=22$)	Stranger ($N=20$)
Vocal			
Screams	0.45	0.91	0.65
Pant hoots	0.73	0.05	—
Hoots	0.09	0.05	—
Pant grunts	—	0.05	0.05
Barks	0.27	0.05	0.20
Other calls	0.09	—	—
Gestural			
Drumming	0.18	0.14	0.05
Hunch	0.45	0.77	0.80
Grin	0.27	0.73	0.55
Mount	0.09	0.41	0.25
Embrace	—	0.14	0.15
Kiss	—	—	0.10
Touch	—	0.09	0.05
Finger in mouth	—	0.14	0.05
Display	0.09	0.14	—
Nongestural			
Groom	0.27	—	0.15
Eat	0.18	0.18	0.20

Locomotor Responses

We compared the locomotor behaviour of individuals in the different experimental conditions in terms of the mean change in location relative to the direction from which the playback was broadcast. In the first 20 min, focal individuals moved towards the speaker in all trials with no significant differences between conditions (group members: $\bar{X} \pm SD = 86.0 \pm 222.8$ m; neighbours: 180.0 ± 102.5 m; strangers: 121.3 ± 117.3 m; Friedman test: $\chi^2_2 = 2.8$, $P_{\text{exact}} = 0.367$). One hour after an experiment, focal individuals were still closer to the location of the simulated neighbour than to the simulated stranger, mainly because subjects retreated substantially after having heard a stranger (group members: $\bar{X} \pm SD = 148.3 \pm 293.4$ m; neighbours: 96.0 ± 295.1 m; strangers: -110.0 ± 266.8 m; Friedman test: $\chi^2_2 = 2.842$, $N = 5$, $P_{\text{exact}} = 0.27$; Fig. 1). A nonsignificant trend in the same direction was also present 2 h after the experiment (group members: $\bar{X} \pm SD = 34.0 \pm 888.6$ m; neighbours: 74.0 ± 250.7 m; strangers: -376.0 ± 506.4 m; Friedman test: $\chi^2_2 = 2.211$, $P_{\text{exact}} = 0.387$; Fig. 1). Responses to group members were intermediate at both 60 min and 120 min, and not different from responses to either neighbour or stranger (Wilcoxon signed-ranks tests: all $Z < 1.3$, all $N = 5$, all $P > 0.3$).

Patrolling behaviour, such as silent stalking and travelling in a single row, was triggered in 12 of 22 neighbour trials (54.5%) and in 11 of 20 stranger trials (55.0%), but only in two of 11 member trials (18.2%). There was no significant difference in patrolling between neighbour and stranger trials, but the difference between member and the combined stranger/neighbour trials was significant (two-tailed Fisher's test: $P < 0.05$).

Effects of Group Size, Sex and Rank

Males were significantly more likely than females to call in response to all conditions (Fisher's exact test: member trials: $P_{\text{exact}} = 0.032$; neighbour trials: $P < 0.001$; stranger trials: $P_{\text{exact}} = 0.012$; Table 3), but a male's rank had no effect on his likelihood of calling in any of the conditions (data pooled across all three communities: Fisher's exact test: $P > 0.05$; Table 3). The number of males present also had no effect on the likelihood of females calling when we controlled for stimulus type (stepwise logistic regression, enter method: $\chi^2 = 0.183$, $N = 33$, Nagelkerke $R^2 = 0.009$, $P = 0.915$).

On hearing the pant hoots of a familiar group member, chimpanzees counter-called in all but one trial ($N = 11$; Table 3, Fig. 2), but sample sizes were too small to test for group size effects. When confronted with the pant hoots of a neighbour, chimpanzees counter-called in almost all trials (20 of 22 trials), regardless of the number of males in the party (stepwise logistic regression, enter method: $\chi^2 = 0.765$, $N = 22$, Nagelkerke $R^2 = 0.098$, $P = 0.358$; Fig. 2). In contrast, when confronted with the pant hoot calls of a male stranger, indicating the very significant event of an arrival of a new group, subjects often remained silent (7 of 20 trials), and the likelihood of calling was significantly dependent on the number of males present in the group (stepwise logistic regression, enter method: $\chi^2 = 6.77$, $N = 20$, Nagelkerke $R^2 = 0.395$, $P = 0.033$;

Table 3
Production of loud calls depending on party composition (number of trials)

Playback condition	Alpha male	Beta male	Gamma male	Any male	Any female
Member	4/4 (100)	3/3 (100)	3/4 (75)	7/8 (88)	1/5 (20)
Neighbour	7/12 (58)	6/11 (55)	8/11 (73)	20/22 (91)	4/15 (27)
Stranger	10/16 (63)	6/10 (60)	2/6 (33)	12/19 (63)	2/13 (15)

Numbers in parentheses are percentages.

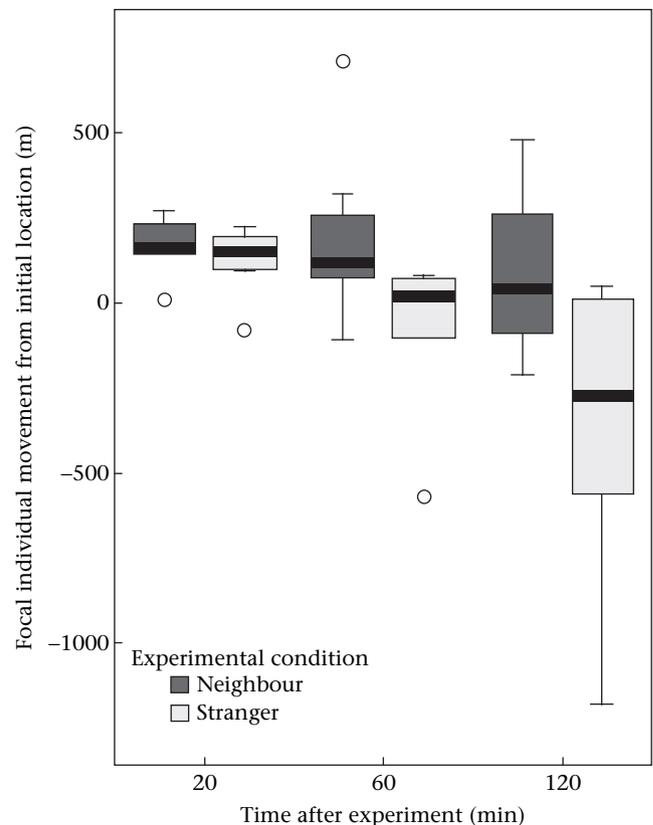


Figure 1. Locomotor responses of chimpanzees after playbacks of pant hoots from neighbour or male strangers relative to the playback speaker. Boxes and horizontal lines are medians and interquartiles, vertical lines are ranges and circles are outliers.

Fig. 2). Calling was only common if the party contained at least three adult males.

DISCUSSION

We found that chimpanzees discriminated between pant hoot vocalizations of familiar group members, neighbours and strangers. Familiar group members mainly triggered pant hoot replies, whereas neighbour and stranger trials mainly caused screams. Neighbours and strangers elicited a wider range of gestural signals than familiar group members. Across conditions, males responded more strongly than females. Male party size had an effect on responses to strangers but not neighbours, and neighbours were approached more closely.

Our study on cross-group recognition in wild chimpanzees is closely related to earlier work conducted with birds and monkeys (e.g. Brooks & Falls 1975; Cheney & Seyfarth 1982). Our contribution is relevant because of the unusual fusion-fission social organization of wild chimpanzees, which is very different from that of most other animals. Most previous studies have demonstrated vocal recognition in species living in stable groups or pair bonds (e.g. Brooks & Falls 1975; Lambrechts & Dhondt 1995). Individual neighbour recognition has mostly been shown in monogamous

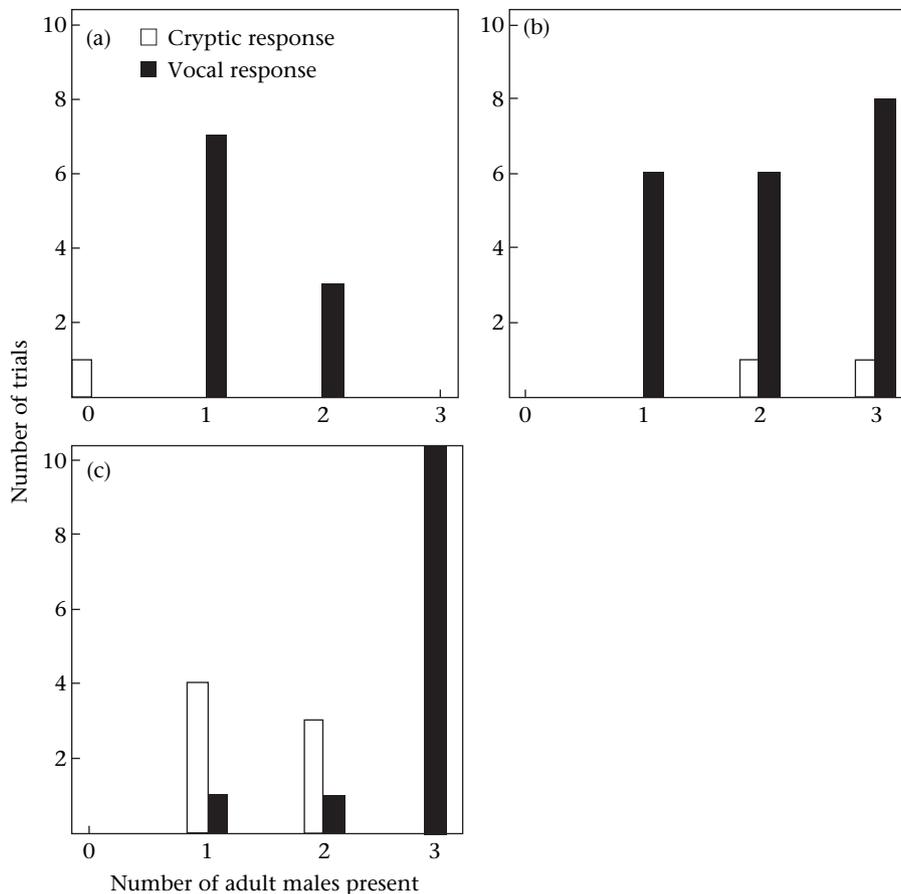


Figure 2. Nonvocal (cryptic) and vocal responses of subjects to playbacks of pant hoots of (a) group members, (b) neighbours and (c) strangers as a function of the number of males in the party, which ranged from zero to three in the experiments.

bird species, where the number of neighbours is limited and relatively stable over time (Falls 1982; Lambrechts & Dhondt 1995; Stoddard 1996).

In chimpanzees, the problem of individual recognition of out-group members is vastly more complex, not only because of sheer group size but also because of their complex social system. Wild chimpanzees typically interact with up to six different neighbouring communities, indicating that individuals would have to discriminate between 25 and 50 neighbouring males based on their pant hoot vocalizations. Intergroup interactions are an important aspect of chimpanzee social life with profound fitness consequences (Nishida et al. 1985; Goodall 1986; Williams 2000; Wilson & Wrangham 2003) and vocal recognition is likely to play a crucial role because of the very limited visibility in their natural habitat. As with many other species, the social behaviour of chimpanzees is not confined to intragroup interactions within a community, but includes relations with conspecifics that are not part of the community (Cheney 1987). Our study thus contributes to this relatively poorly understood area of social behaviour towards a better understanding of how animals classify and remember one another as individuals or groups (Mitani 1994; Uhlenbroek 1996; Crockford et al. 2004).

How can chimpanzees recognize the calls of so many individuals, particularly those of neighbouring individuals, and how do they discriminate them from calls of unfamiliar individuals? Interactions between neighbouring groups occur about once every 2 weeks and they are often limited to vocal exchanges, suggesting that individuals have considerable learning opportunities over time

(Boesch & Boesch-Achermann 2000; Crockford et al. 2004). Recognition of group-specific calls provides one possible explanation and there is some evidence that chimpanzee males converge on group-specific versions of their pant hoot vocalizations (Crockford et al. 2004). Another possibility is that individuals recognize all their neighbours individually. Crockford et al. (2004) provided evidence that males of the three contiguous communities studied here produce individually distinct pant hoots, with differences encoded in both temporal and frequency variables. In mammals, extensive networks of vocal recognition have so far only been described for African elephants, *Loxodonta africana*, which, like chimpanzees, have highly fluid social systems, complex mental capacities, and exhibit long-distance vocal communication (McComb et al. 2000). Individual recognition of neighbours would seem highly beneficial in species where subgroups range independently of each other and in a dense forest habitat where visual identification is not possible beyond 20 m and where encounters are unpredictable.

The ability to discriminate neighbours from strangers is widespread in animals, typically referred to as the 'dear enemy' effect. The general finding is that territorial animals respond less aggressively to neighbours than to strangers, and this is usually explained by differences in familiarity or perception of threat (Muller & Manser 2007). For example, Eurasian badgers, *Meles meles*, discriminate their own scents from those of neighbours and strangers (Palphramand & White 2007). In our study, contrary to the predictions of the 'dear enemy' effect, response patterns to strangers were much more cautious than to neighbours, which

triggered more aggressive responses (see also Temeles 1994). It is important to point out that encountering a group of strangers must be a rare event in chimpanzees, owing to their male philopatric social system. In more than 30 years of observation in Taï, the territory boundaries of the study groups remained remarkably stable and we never observed a natural encounter with a group of strangers, although it is possible that deep invasions of nonadjacent groups may have happened without being noticed. Despite their lack of experience with strangers, the chimpanzees immediately behaved in appropriate ways, perhaps the result of inferential abilities.

Whatever the exact underlying cognitive mechanism, our results showed that chimpanzees responded differently to calls of familiar group members and calls of individuals who were not part of their own community. Pant hoots of familiar group members elicited a relatively narrow range of responses, mainly other pant hoots, with few other vocal signals, suggesting that subjects did not judge this event as socially highly significant or disturbing. Responses were very different when subjects heard the pant hoot vocalizations of neighbours or unfamiliar strangers. Here, subjects responded with screams, although for strangers this was only true when three adult males were present. Subjects also produced a range of gestural signals in response to neighbours and strangers and engaged in a range of social behaviours that generally functioned to reassure social bonds (Table 2). Another difference emerged in the subjects' locomotor responses to the three stimulus types. Although all three conditions triggered immediate approaches, stranger calls soon led to retreat in contrast to responses to neighbours. Differences in the vocal and locomotor responses to simulated neighbours and group members suggest that chimpanzees discriminate individuals based on their pant hoot vocalizations not only within their own community but also between communities.

Vocal, gestural and locomotor responses to neighbour and stranger simulations resembled some aspects of territorial behaviour as reported from natural intergroup encounters. Individuals either sought to confront the intruder or they retreated, although the reasons for this difference remained undetermined. In the Kanyawara community of Kibale forest, Uganda, males counter-called to playbacks of male strangers' pant hoots when their party size was larger than three (Wilson et al. 2001), a group size effect also found in our study. However, in both cases the playback stimuli consisted of pant hoots of unfamiliar strangers and it is conceivable that subjects were reluctant to approach individuals with whom they had no prior history of interactions and whose group size they did not know. At both study sites, males were cautious to reveal their presence if they were alone or with just one partner. Crucially, we did not find this effect in the neighbour condition (Table 2, Fig. 2), suggesting that intergroup interactions with neighbours follow different rules and are probably not solely or predominately influenced by number assessment Wilson et al. (2001).

Chimpanzee females regularly produced vocalizations to neighbours and strangers, demonstrating that both sexes participate in territorial behaviour, although males called significantly more, in line with their generally higher levels of engagement in territory defence (Boesch & Boesch-Achermann 2000; Kitchen & Beehner 2007). In contrast to other studies, we found no effect of male rank on the likelihood of calling in any condition, but this may be because we were only able to monitor small male parties (Wilson et al. 2007).

From a methodological point of view, our study is relevant as one of the first demonstrations that playback experiments with wild chimpanzees are feasible and can add to our understanding of their natural behaviour (see Appendix for ethical implications

of conducting playback experiments with wild apes). Vocal information is likely to be more effective than visual information for long-distance identification of conspecifics. The playback technique has been used successfully to investigate vocal recognition in animals, including several primate species, but not usually with great apes (grey-cheeked mangabeys, *Lophocebus albigena*: Waser 1977; vervet monkeys, *Chlorocebus aethiops*: Cheney & Seyfarth 1980, 1982; pygmy marmosets, *Cebuella pygmaea*: Snowdon & Cleveland 1980; grey and lar gibbons, *Hylobates muelleri*, *H. lar*: Mitani 1985; Raemaekers & Raemaekers 1985; mantled howler monkeys, *Alouatta palliata*: Whitehead 1989; squirrel monkeys, *Saimiri sciureus*: Biben 1993). We have demonstrated that wild chimpanzees are able to associate particular pant hoots with particular classes of individuals, and that they respond in different ways to the calls of individuals with varying group membership status. Whether this ability to discriminate was due to recognition of specific individuals or of community-specific pant hoot variants is for future studies to resolve.

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APPENDIX

Ethical implications for conducting playback experiments with free-ranging apes and other nonhuman primates

Playback experiments with free-ranging primates provide a powerful tool when trying to assess the causal role of vocalizations and other acoustic stimuli in governing animal behaviour. Over the past 30 years, the technique has been successfully used in numerous field studies, particularly with free-ranging monkeys. Despite all this progress, the methodology is not uncontroversial and often raises ethical issues. From a scientific point of view, the main purpose of a successful playback experiment is to use acoustic stimuli to simulate a natural event in order to study systematically the behavioural effects and their underlying governing processes. Ethical issues arise if the event to be simulated requires particularly costly or dangerous coping responses, or if the simulated event has long-term social consequences, which requires researchers to take informed ethical decisions.

In our case, ethical issues arose because playbacks of pant hoots of neighbours and strangers simulated the presence of another group, and this could have affected their future interactions in a negative way. In our view, these and similar experimental manipulations are justifiable provided they simulate a natural situation and give individuals the opportunity to select an appropriate behavioural strategy. Hence, a first key point to consider is that the frequency of the experimental manipulations is comparable with the naturally observed frequency of the event, a variable that we took into account when designing the study. At Tai, neighbouring groups have been observed to engage in intergroup interactions on consecutive days and up to eight times in a given month.

We also monitored the subjects' reactions continuously to see whether the manipulations had any effect on the natural events they were simulating. In our case, a particular worry was whether the playback experiments might lead to deteriorating relationships between two neighbouring communities. We were able to confirm that neither in the year before, during, nor after the playback experiments did we observe any lethal intergroup aggression in the three communities studied. The only case of lethal intergroup aggression that we recorded was one instance of infanticide 1 year and 3 months after the last playback experiments (Boesch et al.

2008). A second case of lethal intergroup aggression (killing of an adult male in the same community) occurred 4 years and 9 months after the last playback trial (March 2005; Boesch et al. 2008). These events occurred in one of the communities and as part of natural social changes within the community (Boesch et al. 2008).

We also checked for more subtle long-term effects. Territory size of one of the communities increased during the period of this playback study but the process was already ongoing before the experiments, suggesting that it was the product of other variables, particularly the number of adult males and their relative fighting power (Lehmann & Boesch 2003; Boesch et al. 2008). During the playback study, territory use (as assessed in terms of the centre of activity) remained stable with about 35% of the territory used as core area. We also measured the frequency of intergroup encounters in the three communities (Table A1). As a general pattern,

encounter rates did not increase in the years following playback experiments, which argues strongly against the hypothesis that our playback stimuli caused intercommunity violence. A much more likely explanation is that changes in intergroup interactions were the result of ongoing changes in the social and demographic variables of these communities.

In sum, we were unable to find any disquieting effects of our manipulations and no evidence that they were harmful to the animals, either short-term or long-term. Chimpanzees responded to our playback stimuli in adaptive ways, which also matched natural observations, but because their experiences were not followed up by subsequent events, they soon returned to their normal daily activities and we were unable to observe any long-term effects. We are thus confident that our study has had no unacceptable negative impact on our study animals.

Table A1

Observed intergroup encounters before, during and after the playback study

Community	Before* (July 1997–June 1999)	During (July 1999–June 2001)	After (July 2001–June 2003)	Total
North	55	35	12	102
Middle	?	57	15	>72
South	>7	29	14	>50

* Reliable records only available for the North community.