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Context-specific calls in wild chimpanzees, *Pan troglodytes verus*: analysis of barks

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Context-specific calls, which have a distinct acoustic structure and are selectively produced in specific contexts, are a prerequisite for calls that function referentially. Functionally referential calls, which convey information to conspecifics about objects and events in the external world, have been found in a number of species, notably primates. Evidence of context-specific calls in apes, however, is largely absent. We analysed whether the barks of wild male chimpanzees in the Taï Forest, Côte d'Ivoire, are context specific. We examined the acoustic structure of barks, and other calls produced in association with barks, in six contexts, using discriminant function analysis. Chimpanzees produced context-specific signals in two ways. First, they produced two acoustically graded bark subtypes, in hunt and snake contexts, respectively. Second, they produced context-specific signal combinations of barks with acoustically different call types or drums. These signal combinations increased specificity levels in three of the six contexts to over 90%, a level similar to the classic vervet monkey, *Cercophithecus aethiops*, predator alarm calls. Furthermore, specific chimpanzee signals were produced in contexts other than alarm, such as travel and hunting, where the potential benefits of evolving specific calls are less obvious. These signals may convey specific context information to listeners, and thus function referentially; however, to confirm this, analyses of listeners' responses are required. The results show that two strategies for producing context-specific signals seem to have evolved in a species other than humans: chimpanzees produce context-specific bark subtypes and context-specific signal combinations.

The question of the evolution of human language has been the driving force behind many animal communication studies (Marler 1977; Cheney & Seyfarth 1990; Hauser 1996). These studies have aimed to identify similarities and differences between animal communication and human language. For example, besides reflecting the internal state of the signaller (e.g. Smith 1977), calls can provide conspecifics with information about objects and events in the external world (Seyfarth et al. 1980a; Marler et al. 1992). Although such vocalizations are qualitatively different from referential human words, as they carry no implication of intent to communicate on the part of the signaller (Marler et al. 1992), they none the less function referentially. Functionally referential calls have a specific acoustic structure, which is selectively produced in a specific context and elicits a specific response from listeners. Context-specific calls are prerequisites of functionally referential calls, but carry no implication of conveying information to conspecifics about objects and events in the external world. None the less, by examining context specificity of calls, we can address the potential of calls to function referentially, the manner in which a call system encodes specific calls (Marler 1976), and whether certain calls are likely to be more specific in certain contexts, and more common in some species (Macedonia & Evans 1993; Bradbury & Vehrencamp 1998).

Functionally referential calls have been identified in a taxonomically diverse range of species, but in a limited range of contexts. They have been found in contexts with putatively high costs (alarm and social aggression), as well as those involving food. The occurrence of such calls in alarm contexts has been documented in several primate species (Fischer 1998; Zuberbühler 2000, 2001; reviewed in Hauser 1996), suricates, *Suricata suricatta* (Manser 2001) and chickens, *Gallus g. domesticus* (Evans et al. 1993) and in social aggression contexts in two primate species (reviewed in Hauser 1996). Food calls have been reported for chickens (Evans & Evans 1999) and rhesus macaques, *Macaca mulatta* (Hauser & Marler 1993). The specificity of these calls varies between species; for example, vervet monkey, *Cercopithecus aethiops*, alarm calls (Seyfarth et al. 1980a, b) are more

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likely to be produced in the presence of predators than are chicken alarm calls (Evans & Marler 1995).

There is no evidence of functional reference in wild apes, perhaps surprisingly, in the light of its prevalence in other species, and considering the evidence of symbolic signalling in laboratory-trained chimpanzees and bonobos, *Pan paniscus* (Rumbaugh 1977; Savage-Rumbaugh et al. 1993). There is only minimal evidence for context-specific calls in apes' natural communication, which has led some to conclude that ape communication is restricted to conveying information about emotional states (e.g. Tomasello & Call 1997). The only study with evidence of context-specific calls showed that a long-distance chimpanzee call, the pant hoot, had three acoustic variants, produced in three contexts: travel, food and encountering within-community conspecifics (Uhlenbroek 1996). Another study, however, with a different chimpanzee population of the same subspecies, *Pan troglodytes schweinfurthii* (Marler & Hobbett 1975; Mitani et al. 1992; Mitani 1994), found no evidence of context specificity in pant hoots (Mitani 1994).

Functionally referential calls, and context-specific calls, are expected to evolve under certain conditions. First, the higher the costs of transmitting imprecise information, the more specific the association between call and context is likely to be (Bradbury & Vehrencamp 1998). For example, kin at risk in predator contexts may elicit more specific functionally referential calls than will a signaller soliciting support in a less risky intragroup context. The tighter the association between a call and the context, the more reliable the call will be as a context predictor for the listener (Macedonia & Evans 1993).

Chimpanzees are expected to produce both functionally referential and context-specific calls, because they live in dense tropical forest, in a fission–fusion social structure (where individuals can be separated for hours or days at a time). Alerting kin or eliciting support would be advantageous when chimpanzees face predation, dangerous intercommunity encounters and sometimes harsh intracommunity aggression (Nishida et al. 1985; Goodall 1986; Boesch & Boesch-Achermann 2000; Fawcett & Muhumuza 2000; Table 1).

To test for context-specific calls is challenging because of features inherent in the chimpanzee call system. First, chimpanzees mainly use only four call types: screams, grunts, hoos and barks, potentially limiting the number of information 'units' that can be clearly encoded. Furthermore, chimpanzees have a graded rather than a discrete call system, where barks, for example, grade into the other three main call types (Marler 1976; Goodall 1986). Although graded calls may not seem suited to encoding specific information unambiguously, Marler (1976) argued that a graded system has the potential to encode large numbers of information 'units', if the units are perceived in a discrete manner. The human vowel system, for example, is graded, although listeners perceive vowels as having functionally discrete acoustic boundaries (e.g. Rosner & Pickering 1994). This type of auditory processing is not unique to humans. Fischer (1998) showed that even though Barbary macaques, *Macaca sylvanus*, have a graded call system, they distinguish two graded subtypes of bark, each of which is produced in a different alarm context. Thus, although chimpanzees seem to have only four main call types, suggesting that few information units can be encoded, call subtypes may exist.

Another way to increase the number of context-specific calls is to produce specific combinations of calls in specific contexts, a potentially powerful strategy rarely addressed in the literature. Humans, for example, combine calls phonologically (combining sounds in words) or syntactically (combining words in sentences), so that with only a few sounds we can produce an infinite number of information units. When Campbell's monkeys, *Cercopithecus campbelli*, combine a 'boom' call with a functionally referential alarm call, they modify the information normally transmitted by the alarm call (Zuberbühler 2002). Chimpanzee calls often occur in combination with other calls or with drumming, where drumming is an additional long-distance acoustic modality for chimpanzees, produced by beating hands and feet against large resonant buttresses of trees. The species-specific pant hoot, for example, is produced either as a series of hoos or as hoos in combination with screams, barks or drums (Goodall 1986; Mitani 1993). As with Campbell's monkeys, signal combinations may convey different information to single call types.

We investigated whether West African chimpanzees, *P. t. verus*, have distinct call types that are context specific, a prerequisite for functionally referential calls. We analysed barks produced in several contexts, including snake alarm, hunting, travel, intracommunity aggression, encounters with neighbouring communities, and in response to hearing intracommunity subgroups or 'parties' (Table 1). We examined whether subtypes of bark exist and are context specific. We also examined whether barks combined with other call types or drums are context specific, for example whether a bark combined with a scream is more likely to occur in one context than in others.

METHODS

Study Site, Individuals and Data Collection

Chimpanzees from two neighbouring habituated communities were observed between April 1998 and May 2000 in the Taï National Park, Côte d'Ivoire, West Africa (Boesch & Boesch-Achermann 2000; Herbinger et al. 2001). Data were collected from all adult males of the North and Middle communities (Table 1), using continuous focal animal sampling (Altmann 1974), with dawn-to-dusk follows, and ad libitum sampling of nonfocal chimpanzees. C.C. collected 1044 h of data from six adult males: two to three in the North community (one male died during the observation period) and three from the Middle community. Males alternated as focal animals and were observed from a distance of 3–20 m. All vocalizations were recorded with a Sennheisser ME65/K6 directional microphone and windshield and a Sony WMD6C Professional Walkman 3–20 m from the individual.

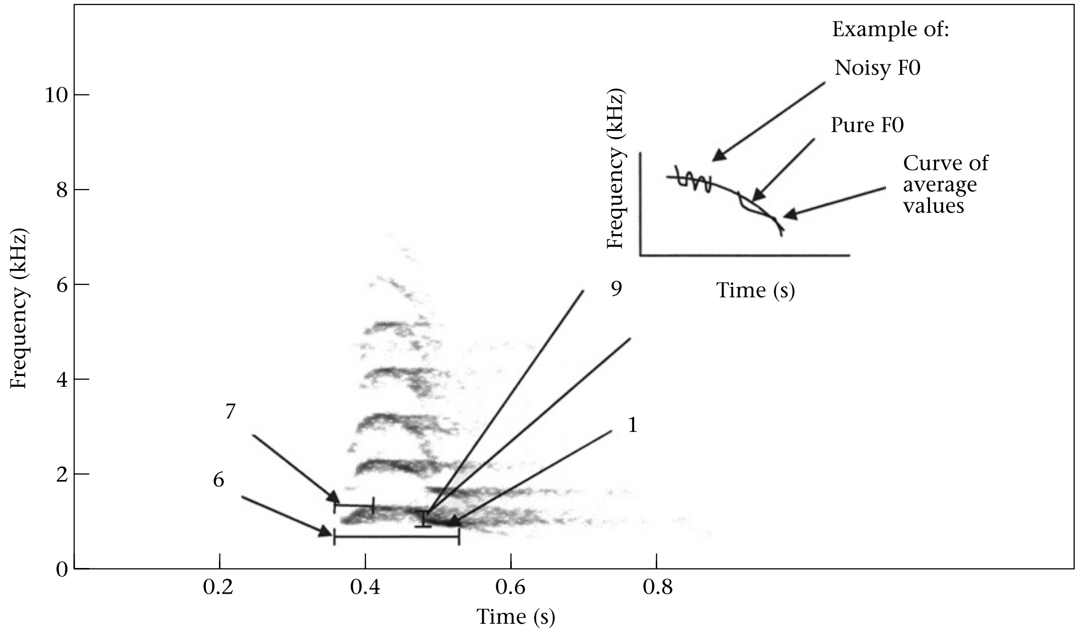

Figure 1. Key bark variables used in the analysis, where numbers indicate variables as numbered in the Appendix.

Table 1. Number of barks per individual per context and context definitions of barking

		Individuals						
		North community			Middle community			
Bark context	Definition	Mac	Mar	Nin	Urs	Leo	Bob	Total
Aggression	Observe or receive aggression from community member*	2	6	11	2	2	7	30
Contact	Hear members of same community but in different party†	5	17	9	13	13	6	63
Neighbour	Hear chimpanzees from a neighbouring community	2	4	3	4	6	4	23
Hunt	Hunt or watch others hunting *Colobus badius* monkeys	0	3	11	0	4	6	24
Snake	Look at snake	4	4	2	2	2	2	16
Travel	When travelling	17	25	9	12	9	4	76
Total		30	59	45	33	36	29	232

*Community: all chimpanzees that share a territory over an extended period of time.
†Party: a temporary community subgroup of variable composition and size.

To determine the context of calling of the focal chimpanzee, we documented all behavioural changes, social interactions and vocalizations, along with the time of occurrence. Events in the forest towards which the target animal looked for more than 10 s were also documented, such as encounters with snakes, leopards, chimpanzees from other communities, and upon hearing alarm calls of other primate species. Using a map, we noted whether the chimpanzee was in the peripheral area or in the core area of the territory when calling. The core area was defined as the part of the home range where the chimpanzees spent 75% of their time (Herbinger et al. 2001). The periphery was defined as the area outside of the core area, and was where encounters with neighbouring communities were most likely to occur.

Ad libitum sampling was conducted when a visible nonfocal male vocalized, and a clear context of calling could be attributed. This was possible without compromising focal sampling when a male that had remained in sight of the target individual and the observer throughout the day was engaged in the same activity as the focal animal, such as grooming or travelling.

Bark Structure and Contexts

We defined a bark as a spectographically dome-shaped call (Fig. 1), typically shorter and with a lower frequency range than a scream, that sounded like ‘waa’, ‘waaoo’, or ‘aaoo’ to the human ear. A bark bout was defined as all calls that were produced with a bark, with less than a 2-s pause between calls. Calls after a silence of 2 s were considered to be a new bout.

Barks were not common; focal individuals produced on average 0.3 barks/h. We analysed calls from six contexts (Table 1). Barks produced in two additional contexts were excluded from the analysis, because of insufficient data: seeing or hearing a leopard, and in response to alarm calls of other primate species (mainly *Colobus badius*, *Colobus* *polykomous* and *Cercopithecus diana*). Half of the bark contexts were rare, occurring on average 0.3, 1.5 and 3 times every month for snake, hunt and neighbour contexts, respectively (calculated over 24 months from 552 observation days).

Barks were produced either as single elements, that is, a single voiced exhalation (59% of barks analysed), or as panted barks, where series of voiced exhalations were joined by voiced inhalations (41%). Single barks consisted of one to three connected segments, where the single voiced exhalation was always present, and 29% were accompanied by a voiced inhalation immediately before or after the voiced exhalation. Furthermore, barks were either produced alone (36%), or in association with other vocalizations (64%), such as at the end of pant hoots and pant grunts, or interspersed with screams or grunts.

Analysis

The analysis involved two steps: (1) acoustic analysis of barks and associated call types and drums within the same bark bout and (2) statistical analysis.

Acoustic analysis of barks

We selected for analysis only barks that met the criteria of certainty of signaller and unambiguous context, without overlap with other signallers or masking background noise. When possible, we selected the first bark in a bark bout. To avoid pseudoreplication, we included only one bark per signaller per event, except in three rarely occurring contexts, snake, hunt and neighbour encounters, where we used two barks per signaller per event. One event lasted for the duration of an uninterrupted behaviour, such as travelling or hunting. We selected 232 barks out of 435 bark events for analysis.

Acoustic analysis was carried out using two methods. First, we extracted 28 temporal and frequency measurements from single exhaled bark elements (Appendix). The bark selected from each call (e.g. Fig. 1) was digitized with Canary 1.2.4, with sampling frequencies of either 22.05 kHz/16 bits or 44.1 kHz/16 bits (Charif et al. 1995). Downsampling using an antialiasing filter and fast Fourier transforms were conducted with the signal sound analysis system (1024-pt FFT; time resolution: 5 ms; frequency range: 8820 Hz; frequency resolution: ca. 22 Hz; Beeman 1996). Using an acoustic software program, LMA, developed and customized by Hammerschmidt (1990), we calculated values at 5-ms intervals throughout each call. Second, we extracted five temporal and descriptive measures of the extended bark structure (Appendix), using Canary 1.2.4 (filter bandwidth: 349.7 Hz; time resolution: 0.73 ms; frequency resolution: 21.53 Hz): number, rate, total duration, presence of panting (audible inhalations between barks) and number of bark syllables.

Acoustic analysis of bark bout variables

In addition to barks, we also included as variables the presence/absence of other call types or drumming produced in the same bark bout and the presence/absence of a further bout of barking following the analysed bout (Appendix).

Statistical analysis

Determining variables influenced by context. To remove variables with no predictive power for context, we tested the 32 continuously distributed variables (Appendix), using a repeated ANOVA with replicates (rANOVA, programmed by R. Mundry). An rANOVA was preferred over a univariate ANOVA, because it allowed us to use a mixed model, which included individuals as a random factor, while testing context as a fixed factor (Sahai & Ageel 2000). Acoustic variables for which individual effects were stronger than context effects were excluded. Similarly, we excluded variables with a significant interaction of individual and context effects. Because we were using an exploratory analysis, we used replicate measures for the same individual without creating a type 1 error. To account for replicated observations, data were balanced with a minimum number of replicates (two barks per individual per context for every variable), which prevented overproportional influence of one individual. The process of balancing, however, excluded up to 80% of the data and so we repeated the rANOVA, with each new test randomly selecting a different balanced data set. After 1000 tests we could be sure that all the data had been tested. When 95% of the 1000 repeated rANOVA tests showed significant effects for context, and no significant individual or interaction effects, we concluded that the tested dependent variable showed differences between contexts. As two individuals did not have barks in the hunt context, we tested each variable twice, once with balanced data for six individuals and five contexts and then with balanced data for four individuals and six contexts. We excluded from the analysis two dependent variables with values that did not approximate a normal distribution, even with transformation.

We then used principal components analysis to exclude correlated variables (SPSS 1999). Correlated variables loaded on to nine separate components and we selected the variable with the strongest significant context effect from each component for further testing. Post hoc tests (SPSS 1999) were carried out on these variables, using Bonferroni correction, to determine which context had the strongest effect. We used the balanced data set from the rANOVA that produced a P value closest to the average P value calculated from the 1000 tests in each case.

We tested categorical variables as for continuous variables except that instead of an rANOVA we used a generalized linear model (GLM, Statistica 99 Edition, StatSoft 1999) to identify context effects. The GLM allows a model to have a nonlinear relation between dependent and independent variables, both of which can have categorical or continuous data distributions (McCullagh & Nelder 1989). Each acoustic variable was simultaneously tested for context and individual effects, using a multinominal error distribution and a log-link function (McCullagh & Nelder 1989). All calls were included in each test. Acoustic variables with significant context effects, but with no or smaller individual effects, were

Table 2. Chimpanzee barks: acoustic variables significantly influenced by context

	Repeated two-way ANOVA with replicates (1000 tests)				
Continuous variables	Mean *F*	% Significant tests	No. of subjects and contexts	No. of calls	Context differences
Single bark					
Minimum F0 (Hz)	4.53*	100.0	6,5†	216	S<(C) N T
Tonality (Hz/ms)	7.58*	100.0	6,5†	216	S<A N T
Position of maximum F0 (%)	7.52*	99.6	6,5†	216	S<C N T N>(A) S
Bark duration (ms)	2.51*	100.0	4,6	176	H<A C N S T
Extended bark					
No. of barks (log)	2.06*	99.5	6,5†	216	S>A C T

Contexts: H=Hunt, S=Snake, N=Neighbour, T=Travel, C=Contact, A=Aggression. See Fig. 1 and Appendix for variable definitions. *df*=4,20 except for bark duration (5,15).

*Mean $P<0.01$. Context differences were calculated from post hoc tests using Bonferroni correction where $P<0.05$; parentheses indicate $P<0.1$. Variables showed no individual or interaction effects.

†Hunt excluded.

Table 3. Chimpanzee bark bouts: acoustic variables significantly influenced by context

Categorical variables	W_5	Context differences
Extended bark		
No. of syllables	36.0*	T>C H S
Pant versus single	16.39*	H S<A C T N
Bark bout		
Drum	42.32*	T>A C H S
Pant grunt	35.0*	A>C H N T S
Second call bout	59.9*	A<C H N T S

W=Wald statistic from generalized linear model.

*$P<0.01$. Context differences are shown when parameter estimates were $P<0.05$. Variables showed no individual or interaction effects.

tested with discriminant function analysis (DFA). Parameter estimates from the GLM were used to locate the contexts accounting for the differences in variance. Weaker remaining correlated categorical variables or continuous and categorical variables were removed in the next stage of testing.

Determining context-specific calls. The tests described so far examined acoustic variables separately; however, acoustic discrimination of calls by humans and other animals rarely depends on a single acoustic variable. Therefore we tested continuous and categorical variables influenced by context in a simultaneous DFA (Bortz 1993). Variables were combined into $n-1$ discriminant functions (where n is the number of contexts in the analysis) which, when plotted, showed the grouping patterns of the calls (Fischer et al. 2001). Based on the discriminant functions, calls were assigned to their appropriate group or to another group, producing a percentage of correct classification.

We tested two sets of variables in the DFA: bark variables and bark variables together with the bark bout variables. The bark variables were tested to assess whether the barks themselves are acoustically distinct in specific contexts. The bark bout variables were then added to assess whether chimpanzees may gain additional information from listening to associated call types in the same bark bout. Each analysis randomly selected balanced data sets (again using two calls per individual per context) which were used to create the discriminant functions. This produced the original classification result. For the external classification, all the remaining calls (80% of the total data) were then classified according to these functions. Variables with a weak correlation to the discriminant functions were removed and the DFA was repeated as before. In this way, we removed weaker variables correlated with others. When the external classification result was higher than expected by chance (with six contexts, external classification at chance levels was expected to be 32.8%), it indicated that specific calls were produced in specific contexts.

As a final step in the analysis, we determined signal specificity, that is whether the most commonly produced signal structure in a context was produced exclusively in that context. We named the most common signal produced in a context after the context itself, such as ‘neighbour’ signal. We did this for the sake of brevity and not to imply that the call refers to that context, as emphasized by the inverted commas around the context. To identify the most common signal type, we converted continuous variables into categorical data. The cutoff point for creating the categories was defined as the last nonoutlier value of the variable, within the context creating the significant difference. This method, of using actual values from acoustic variables, for calculating how precise the association is between the most common signal type and its context, was preferred as a more direct measure over the derived discriminant function scores.

For signal specificity, we calculated the percentage of occasions on which the most common signal type was

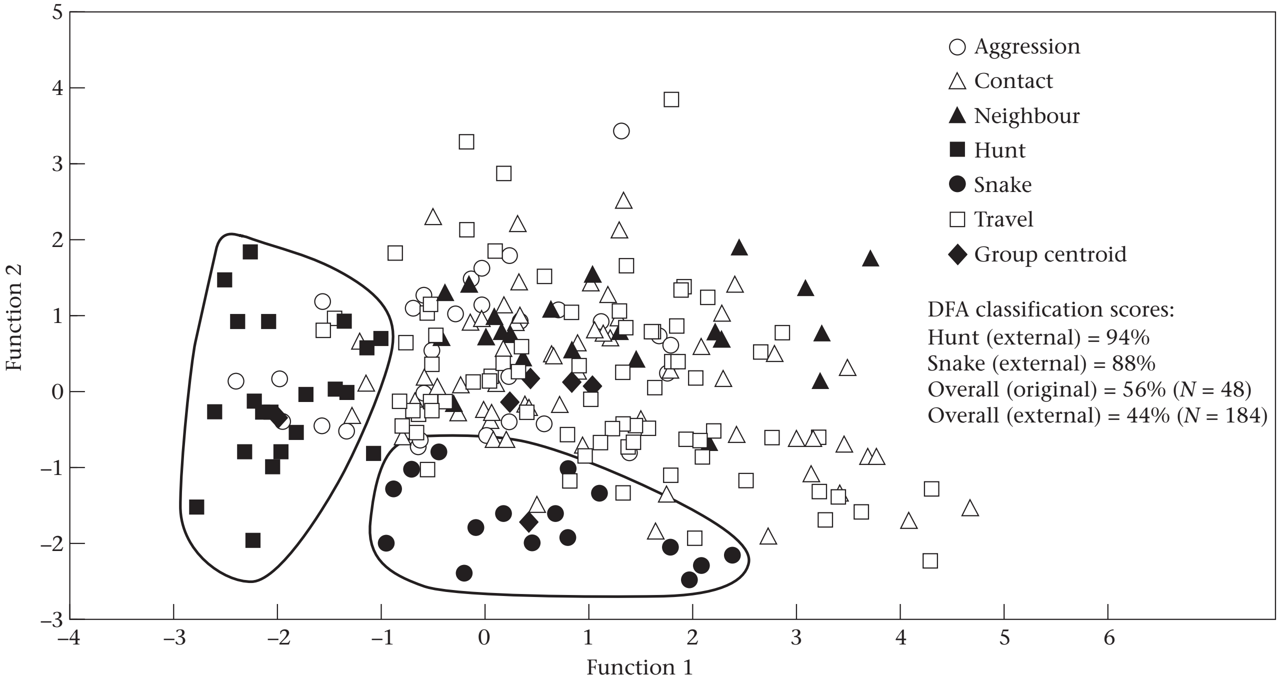

Figure 2. Context-specific barks. The discriminant function analysis plot, using three bark variables, shows the distribution of the discriminant scores for six contexts. Function 1 was correlated with duration, and function 2 with tonality and the position of the maximum F0. The three bark variables used to generate the discriminant functions are described in Fig. 1 and the Appendix. The circles were added by hand to aid identification of clusters.

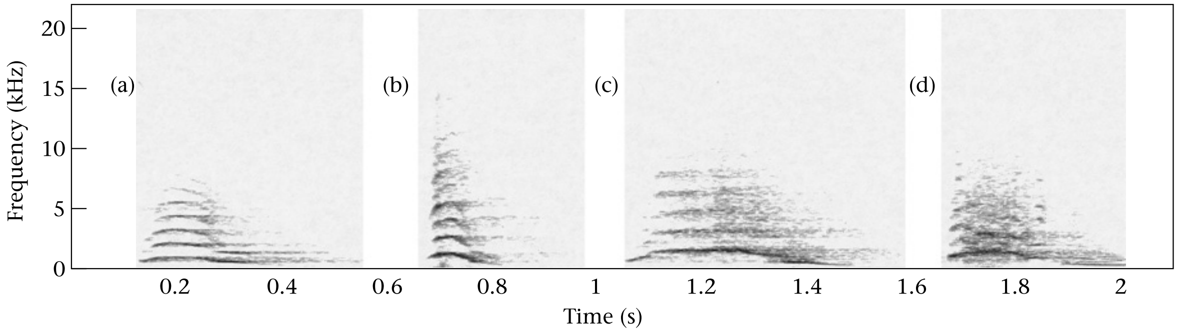

Figure 3. Spectrograms showing barks produced in four contexts: (a) 'snake' bark; (b) 'hunt' bark; (c) 'neighbour' bark (d) 'travel' bark. Barks (b), (c) and (d) were produced by male Mar and (a) by male Mac.

produced in its specific context. We compared these percentages to those found with the alarm calls of vervet monkeys (Seyfarth & Cheney 1980) and chickens (Gyger et al. 1987). We also determined context specificity, that is, how likely it was that each context actually elicited its signal type. We calculated the percentage of occasions on which each of the six contexts elicited its signal type and not any other signals.

RESULTS

Specificity of Barks

Of the 33 acoustic variables, four uncorrelated variables describing the bark itself and three variables describing the extended bark structure were significantly affected by context (Tables 2, 3). For these seven variables, the context effects were stable between individuals and between communities.

Two bark subtypes were identified: barks produced in hunt and snake contexts could be discriminated from those given in the other four contexts as well as from each other (Fig. 2). The barks produced in the remaining four contexts, travel, aggression, neighbour and contact, showed minimal discrimination from each other, indicating a generic bark type. Figure 3 shows spectrograms of barks produced in different contexts.

Barks produced in hunt contexts were short, but those produced in snake contexts were long, with pure tonality and an early position of maximum fundamental frequency (Table 4, Appendix). Context specificity, that is, the percentages of occasions on which hunt and snake contexts elicited their bark subtype, was high (92 and 88%, respectively; Table 5). The signal specificity, that is,

Table 4. Characteristics of the most common signal types produced in each context: bark subtypes and bark and bark bout combination types

Context	Characteristics of signal types
Bark subtypes	
Hunt	Bark: short
Snake	Bark: long+pure tonality+early position of maximum F0
Bark and bark bout combination types	
Hunt	Short bark+second call bout+no drum
Snake	Long bark+pure tonality+early position of maximum F0+second call bout+no drum
Neighbour	Long bark+high F0+second call bout±drum
Travel	Bark+Drum
Aggression	(1) Pant grunt+one call bout+no drum+few barks (2) No pant grunt+one call bout+no drum+many barks
Contact	Long bark+no pant grunt+no drum+few barks

Bark duration: short<170 ms<long; tonality: pure<20 Hz/ms<noisy; position of maximum F0: early<0.25<late, where 0.25 is a proportion of call length. See Fig. 1 and Appendix for variable definitions.

Table 5. Signal and context specificity of barks and signal combinations in Taï chimpanzees

	Classification of signal types							Context specificity (%)
Context	H	S	N	T	A	C	U	
Barks								
Hunt (H)	**22**	—					2	92
Snake (S)	—	**14**					2	88
Neighbour (N)	—	—					23	
Travel (T)	3	4					56	
Aggression (A)	9	0					17	
Contact (C)	1	2					53	
Signal specificity (%)	63	70					—	
Barks and bark bouts*								
Hunt (H)	**17**	—	—	—	2	1	1	81
Snake (S)	—	**13**	—	—	1	—	2	81
Neighbour (N)	—	—	**23**	—	—	—	—	100
Travel (T)	—	—	12	**62**	—	1	—	83
Aggression (A)	—	—	—	—	**28**	3	—	90
Contact (C)	—	1	8	6	14	**31**	3	49
Signal specificity (%)	100	93	51	95	76	86	—	

U=Undefined. Signal specificity is the percentage of signal types produced in their designated context (i.e. columns). Context specificity is the percentage of designated context occurrences eliciting their signal type (i.e. rows). Signal types correctly classified in their designated contexts are shown in bold.
*Four calls were excluded, because not all variables were measurable.

the percentages of ‘hunt’ and ‘snake’ barks that occurred in their specific context, was lower, 63 and 70%, respectively. Thus, ‘hunt’ and ‘snake’ barks were not produced exclusively in hunt and snake contexts, but reflected a degree of acoustic overlap that is expected in a graded system.

Specificity of Barks and Bark Bouts

Three variables from the associated signals in the bark bout were significantly affected by context (Table 3). When these were analysed together with the significant bark variables (Table 2), the overall correct classification of calls produced in the six contexts was increased from 44% (Fig. 2) to 71% (Fig. 4; $\chi^2_1=21.63$, $P<0.001$). Signal combinations clustered for five of the six contexts (except contact context; Fig. 4). The clusters indicate that the signal combinations, made up of barks combined with other call types or drums, were produced in specific contexts.

Table 4 gives the characteristics of the most common signal types occurring in each context. Context specificity was 80–100% for five of the six contexts (Table 5). Signal specificity was 86–100% for four contexts. Adding bark bout variables increased the signal specificity of ‘hunt’ and ‘snake’ calls from 63 to 100% and from 70 to 93%, respectively. A combination of high signal specificity and high context specificity was evident in three contexts:

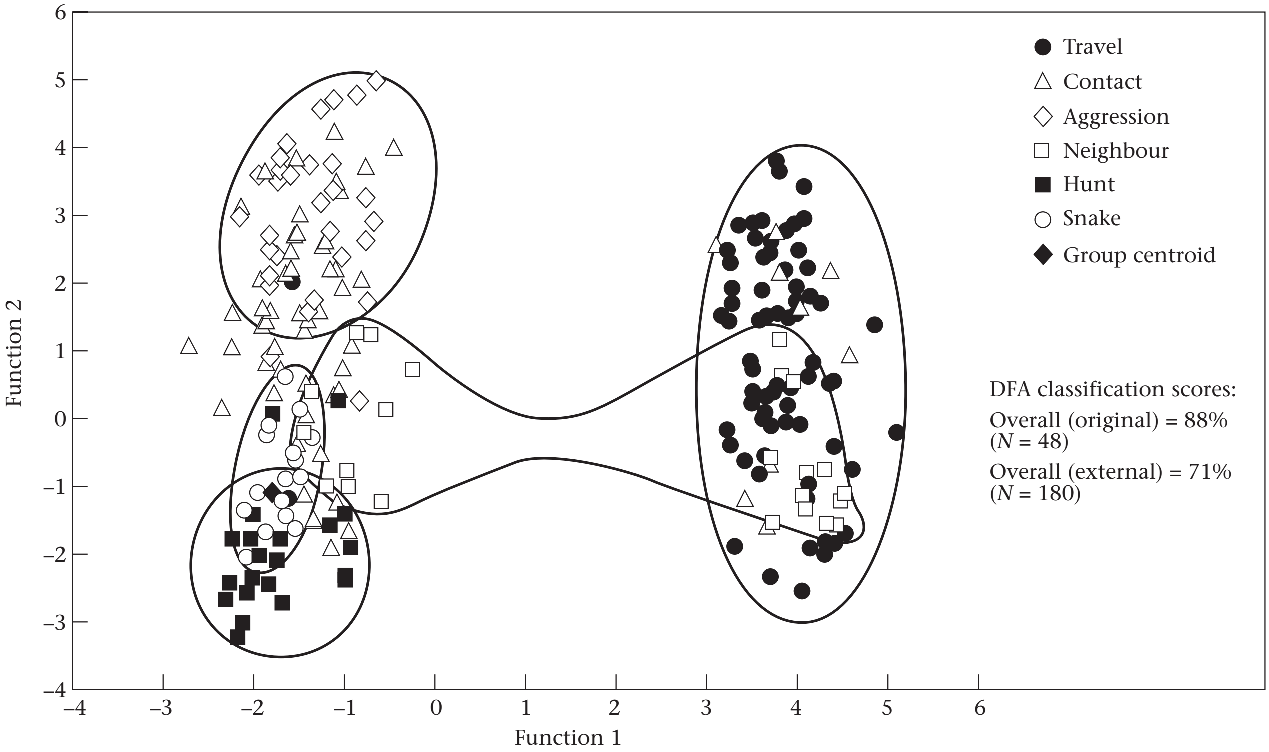

Figure 4. Context-specific signal combinations: barks combined with other calls and drums. The discriminant function analysis plot, using four bark and three bark bout variables, shows the distribution of the discriminant scores for six contexts. Funtion 1 was correlated with drum, minimum F0, duration and tonality, function 2 with the absence of the second call bout, duration, tonality and the presence of a pant grunt. The four bark and three bark bout variables used to generate the discriminant functions are described in Fig. 1 and the Appendix. The circles were added by hand to aid identification of clusters.

travel, hunt and snake. Compared with other contexts, contact contexts elicited its signal type the least (49%). Although most 'contact' calls were produced in contact contexts, other call types were produced more in contact contexts than 'contact' calls.

Because of the high percentage of 'neighbour' calls occurring in travel and contact contexts, we checked the signaller's location at the time of calling. Chimpanzees were more likely to produce 'neighbour' calls in the peripheral area of their territory, regardless of the context in which the calls were produced (exact chi-square goodness of fit: $\chi^2_1=13.1$, $N_{\text{periphery}}=12$, $N_{\text{core area}}=8$, $P<0.01$, corrected for time spent in the peripheral area). Most neighbour encounters (93%) occurred on the periphery.

DISCUSSION

Two acoustically different subtypes of bark were detected in the hunt and snake contexts, respectively, indicating that chimpanzees produce moderately specific barks in specific contexts. Signal combinations of barks with other call types or drums showed much higher signal specificity, showing for the first time that chimpanzees produce highly specific signals in specific contexts. Combining signals is a potentially powerful adaptive strategy for conveying precise, context-specific information, one that has been little explored in the literature.

The barks produced in hunt and snake contexts showed moderate acoustic differences, indicating that signallers can create fuzzy acoustic categories within a graded call type. Although acoustic overlap was apparent, as is expected in a graded system, the results support Marler's (1976) hypothesis that graded calls can be subdivided into functionally discrete subcategories.

We also found different combinations of barks with other call types or drums, which were restricted to specific contexts: travel, hunt and snake. Although the specificity of the graded 'hunt' and 'snake' bark subtypes alone was not strong, specificity was markedly increased when barks were tested in combination with drum and call bout variables. This supports the hypothesis that combining different signals is a strategy for increasing the number of information units within a graded system. Further analysis of the chimpanzee signal system is needed to determine whether added signals may function as phonological or syntactic units.

Both the bark subtypes and the signal combinations were acoustically stable, not only between individuals but also across neighbouring communities. Thus, if listeners extract information from these calls, the information is likely to be similar, regardless of whether the caller is a male community member or a neighbour.

Most of the misclassified calls derived from the contact context. Although 86% of all 'contact' signals were produced in contact contexts, they were produced less often in contact contexts than were other signal types. By definition (Table 1), the contact context is likely to contain components of other contexts, for example, chimpanzees responding to absent conspecifics may also be travelling, in which case the designated 'contact context' may not operate as an independent category.

Another source of misclassified calls could be attributed to the production of 'neighbour' calls in travel and contact contexts in addition to actual neighbour contexts. 'Neighbour' calls were more likely to be uttered in travel and contact contexts, when chimpanzees were in the peripheral area of their territory, indicating that 'neighbour' calls may have a general territorial function, in addition to their use during neighbour encounters. If this hypothesis is true, 'travel' signals may show considerably higher context specificity than indicated in Table 5. Similarly, the production of 'aggressive' calls in hunt and snake contexts may reflect the occasional direction of aggression towards the other species in these contexts (Table 5).

Chimpanzee calls showed levels of signal specificity comparable to functionally referential alarm calls of other primate species, even in nonalarm contexts. They were correctly classified in snake, travel and hunt contexts, with 93–100% accuracy (Table 5). Functionally referential vervet monkey alarm calls, produced to snakes, eagles and leopards, showed 75–95% levels of signal specificity, respectively (Seyfarth & Cheney 1980). The calls of both primate species showed much higher specificity than functionally referential chicken alarm calls (35% for aerial predator calls, Gyger et al. 1987; Evans & Marler 1995). Humans also have imperfect specificity, such as saying words in the wrong contexts. In picture-naming tasks, normal human adults have shown 96% specificity levels (Dell et al. 1997; Levelt et al. 1999).

But how specific is specific? Signal detection theory suggests that specific calls are unlikely to occur in their designated context 100% of the time, because of selection pressures on some calls (Bradbury & Vehrencamp 1998). However, specific calls must be reliably produced in a specific context for a clear association to emerge. Comparing across contexts, one might expect specificity to be high when the costs of being nonspecific are high, such as in predator alarm contexts, where kin may be killed if a specific alarm call is not produced. However, the highest specificity in the Taï chimpanzee calls was in hunt contexts, where possible fitness benefits gained from hunting are less obvious and less direct than in alarm contexts. An explanation for this may be that larger brains, with space for more sensory and motor connections, require a lower threshold of costs and benefits for developing vocal specificity (Bradbury & Vehrencamp 1998). Alternatively, animals evolving the production of specific calls in specific contexts maybe more widespread than expected.

Although chimpanzee signals showed high levels of specificity, it remains to be tested whether they serve a referential function. Observational data showed that signals in travel contexts elicited vocal responses and arrivals of chimpanzees from other parties, but signals in neighbour contexts did not. This suggests that listeners may extract different information from different signals. Verification of this hypothesis requires playback experiments to determine whether listeners respond differently to different signals in the absence of the context.

This study has shown that chimpanzees produce context-specific signals in two ways: bark subtypes and signal combinations. Combining these two strategies is a potentially powerful system for encoding vast numbers of information units, a system that this study indicates may not be unique to humans. As many species have graded call systems and combine signals, future research may show that other species also use both of these strategies.

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Appendix: Acoustic Structures

Single bark elements

(1–5) Minimum*, maximum, start, end and mean of fundamental frequency (F0) across all time segments (Hz).

(6) Bark duration* (ms), from start to end of call.

(7) Location of maximum F0 as a proportion of call length*.

(8–9) Maximum and mean* measures of 'tonality' of the F0 (Hz) (the number of times the original curve of the F0 crosses the average, approximates noisy tonality versus pure tonality).

(10) Factor of the linear trend of the F0 across the call (whether the call is rising, falling or flat).

(11) Maximum difference between the trend line and the F0 (Hz).

(12) Mean difference between the trend line and the F0 (Hz).

(13) Maximum frequency of all peak frequencies across all time segments of the call (Hz).

(14) Minimum frequency of all peak frequencies across the call (Hz).

(15) Peak frequency with maximum amplitude across whole call (Hz).

(16) Peak frequency with minimum amplitude across whole call (Hz).
(17–18) Peak frequency at start and end of call (Hz).
(19) Maximum difference in peak frequency in successive time segments (Hz).
(20) Slope of F0 from start to maximum (Hz/ms).
(21) Slope of peak frequency from start to maximum (Hz/ms).
(22) Positive deviation of F0 from the trend line (Hz/5-ms time segment).
(23) Negative deviation of F0 from the trend line (Hz/5-ms time segment).
(24) Maximum F0 − start F0 (Hz).
(25) Maximum F0 − minimum F0 (Hz).
(26) Duration from start to maximum F0 (ms).
(27) Location of maximum peak frequency in call (ms).
(28) Location of minimum peak frequency in call (ms).

Extended bark structure variables

(29) Number of barks in call bout†*.
(30) Total duration of barks†.
(31) Rate of bark production†.
(32) Whether bark was panted or not*.
(33) If bark was not panted whether it was one or multisyllable*.

Bark bout variables

(34) Presence/absence of drums*.
(35) Presence/absence of pant grunts*.
(36) Presence/absence of hoos.
(37) Presence/absence of pant hoots.
(38) Presence/absence of screams.
(39) Presence/absence of grunts.
(40) Ratio of screams: barks†.
(41) Presence/absence of a bout of barking within 2 min of bout end*.

Single bark elements were measured with linear model analysis and were continuously distributed. Extended bark structure and bark bout variables were measured with Canary 1.2.4 and were categorically distributed, except for those marked †, which were continuously distributed. *Indicates uncorrelated variables significantly influenced by context, with no subject or interaction effects. Variable 28 was not normally distributed and so was excluded from the analyses.