

Call combinations in wild chimpanzees

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Summary

By combining different call types, such as barks with screams, individuals have the potential to vastly increase the range of information that can be decoded by listeners. Few animal studies, however, have examined the information content of call combinations compared with the information conveyed by each call singularly. We examined several aspects of call combinations in the repertoire of wild chimpanzees in the Taï Forest, Ivory Coast, including the types of combinations, the contexts and possible functions and compared these with the use of single calls. Almost half of all vocalisations produced by the Taï chimpanzees occurred in combination with other vocalisations or with drumming. A total of 88 different types of combinations were used. Single calls and call combinations were each produced in specific contexts. The contexts in which six of ten combinations were produced differed from the contexts of at least one of the component calls. The contexts in which the combinations were produced varied from the component calls in five different ways, three having potentially novel functions. Two of the three may have an additive function, such that two pieces of information can be conveyed simultaneously, increasing message complexity. This analysis clearly shows that call combinations are an important part of chimpanzee communication. The implications with regard to the evolution of human language are discussed. Testing of the information conveyed by single calls and of call combinations, using playback experiments, is advocated.

Keywords: chimpanzee, communication, information, call combination, context specific call types.

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Introduction

A basic aspect of vocal communication is that listeners decode information contained in the vocalisations of others (Hauser, 1996; Seyfarth & Cheney, 2003). Calls need to vary if different information is to be transmitted and decoded. However, most mammals' calls are innately programmed, such that signallers have limited ability to modify the structure of their calls into new call types (Janik & Slater, 1997). An alternative way of increasing decodable information is to use sounds in combination rather than singularly. The combinatorial power of call combinations can vastly increase the number of different words, in the case of humans (Bickerton, 1990), or songs, in the case of birds (Kroodsma, 1982) and whales (Payne & Payne, 1985), which can be produced. In fact, in terms of more message possibilities, combining sounds is more efficient than producing new sounds (Jackendoff, 1999). Strikingly little research has examined the information content of combined calls compared with single calls (Zuberbühler, 2002).

Calls used in combination have, nonetheless, provoked interest in animal studies probing for 'fossils' of language (Jackendoff, 1999), in particular syntax. All human languages essentially require two types of syntax. In phonological syntax, where strings of sounds are grouped together according to certain rules, the individual sounds themselves do not convey meaning. In lexical syntax, where strings of words are grouped together according to certain rules, the individual words do convey meaning (Marler, 1977; Jackendoff, 1999).

Examples of phonological syntax in animals are not uncommon, especially in the learned songs of birds (e.g., Kroodsma & Miller, 1982) and whales (Payne & Payne, 1985). In primates, the call combinations usually cited are long distance calls, used for regulatory spacing between groups (Marler, 1977). These have been described as stereotyped in structure, so that the combinations occur in a fixed order. Furthermore, the contexts in which the combinations occur differ from the contexts of the component calls (chimpanzee pant hoot: Marler & Hobbett, 1975; gibbon song: Mitani & Marler, 1989; gray-cheeked mangleby 'whoop-gobble': Waser, 1975; blue monkeys 'ka-train': Marler, 1973). As such they have been labelled as a primitive form of phonological, rather than lexical syntax (Marler, 1977).

Since then, there have been tantalising descriptions of call combinations by apes that are not just limited to long distance calls, for example, barks

combined with screams or grunts (chimpanzees: Goodall, 1986; bonobos: Bermejo & Omedes, 1999). However, little quantitative assessment of the extent and possible functions of these calls has been conducted. Crockford & Boesch (2003) found in chimpanzees, that barks produced in combination with buttress-tree drumming occurred specifically in travel contexts or during neighbour encounters. In other primates, there are a few studies that have examined different types of call combinations, their contexts of production and possible functions relative to each call produced singularly (Robinson, 1979, 1984; Cleveland & Snowdon, 1982; Zuberbühler, 2002). In each case the results indicated that primates are using certain forms of 'lexical syntax'.

Robinson (1984) unpacked Marler's (1977) term 'lexical syntax' used to describe call combinations, into two aspects (a) where one call acts as a contextual modifier for the other and (b) where grammatical rules generate combinations of words to form sentences. Call combinations produced in contexts intermediary to their component calls have been described by Robinson (1984) as acting as contextual modifiers. However to date, no examples in animals can be described as having grammatical rules that generate combinations to form sentences.

Examples of contextual modifiers have been found in primates (Cleveland & Snowdon, 1982; Robinson, 1984; Zuberbühler, 2002), wolves (Schassburger, 1993) and willow ptarmigans (Martin et al., 1995). Usually the contexts in which call combinations were produced were intermediary to those of the component calls. For example, in cotton-top tamarins, type E' chirps were produced in general alarm situations and squeaks in general alert situations, other than alarm. The two call types combined were produced in intermediary contexts requiring vigilance but with reduced fear or alarm (Cleveland & Snowdon, 1982).

Zuberbühler (2002) used playback experiments to establish that the responses of listeners changed if a so called 'leopard' alarm call was preceded by a general alert 'boom' call. While diana monkeys produced their own leopard alarm calls on hearing a Campbell monkey leopard alarm, they produced no alarm calls on hearing either a Campbell monkey 'boom' call alone or a 'boom' call followed by a Campbell monkey alarm call. The 'boom' call seems to have modified the information conveyed by the alarm call, and as such is indicative of an early form of lexical syntax.

In another form of contextual modification, a call combination may act as an intensification of the context of the component calls. Schassburger (1993)

documented that although wolves used barks and growls as threats, a bark-growl combination carried a more intense threat than either bark or growl alone.

Clearly, the analysis of single call types relative to call combinations is necessary for ascertaining the functions of call combinations. In summary and in addition to the examples given above, suggested functions, to date, include expression of an intermediary internal state (Robinson, 1984), expressing ambivalence (Schassburger, 1993), refined expression by emphasizing emotional intensity (Schassburger, 1993), or one call acting as a syntactic modifier of another (Zuberbühler, 2002). Alternatively, call combinations may advertise male quality (túngara frogs: Kime et al., 1988). All of these putative functions suggest that information conveyed by call combinations is additional to information conveyed by the single call types, such that call combinations increase the range of information that can be decoded by others.

It is unlikely that call combinations used by any animal approach the complexity of syntax used in human language, particularly in terms of recursion, which involves the limitless embedding of clauses into sentences (Jackendoff, 1999; Bickerton, 2003; Fitch & Hauser, 2004). Nonetheless, comparative research is crucial if we are to resolve what is unique to humans as oppose to what constitutes 'fossils' of human language or language abilities (Jackendoff, 1999; Hauser et al., 2002). As stated above it seems that chimpanzees use a range of call combinations (Goodall, 1986), one of which is produced in specific contexts (Crockford & Boesch, 2003). We further examine the extent of the occurrence of call combinations in the repertoire of wild chimpanzees, the types of combinations that occur, the contexts in which they occur and the possible functions they may have.

Methods

Study site, individuals and data collection

Chimpanzees from two neighbouring habituated groups were observed between February 1999 through to May 2000 in the Taï National Park, Côte d'Ivoire, West Africa (site description in: Boesch & Boesch-Achermann, 2000). Data were collected continuously using focal animal sampling (Altmann, 1974) with dawn to dusk follows, and ad-libitum sampling of non-focal

chimpanzees. All adults of the North community (3 adult males and 10 adult females) as well as all three adult males of the Middle community were included in the analysis. C.C. collected 590 hours of data from the six adult males and 520 hours from 10 adult females. Chimpanzees alternated as focal animals and could easily be followed at a distance of 3-5 m.

All vocalisations were recorded using a Sennheisser ME65/K6 directional microphone and windshield and a Sony WMD6C Professional Walkman at a distance of 3-15 m from the individual.

To determine the context of calling for the focal chimpanzee, each change of behaviour, each social interaction and each vocalisation of, or directed to, the focal chimpanzee was documented with the time of occurrence. Events in the forest that the target animal looked towards for more than 10 seconds were also documented, such as encounters with snakes and chimpanzees from other communities.

Classification of single and combined calls

Single call types were defined as those easily distinguishable from each other by ear. Chimpanzee vocalisations are graded such that each call type has 'pure', easy to categorise, variants such as screams and barks, and 'intermediate' variants such as those acoustically between scream and bark and therefore difficult to categorise. We excluded 'intermediate' variants of all call types from the analysis. We distinguished 15 vocalisations and included one frequently occurring non-vocal signal, buttress tree drumming (Table 1). This classification differs from the two published chimpanzee repertoires at other chimpanzee sites, probably as a result of differing tendencies to lump or split calls into the same or different call categories (32 different call types at Gombe: Goodall, 1986; 11 different call types at Kanyawara: Clark, 1991). Cross-site detailed acoustic analysis accompanied by contextual correlates of calling, for the entire chimpanzee repertoire, is required to resolve this issue.

In addition, we noted combinations of calls and calls with drums (hereafter 'call combinations' for simplicity). We distinguished between single and combined calls as follows: single calls were defined as those occurring as single elements or a series of elements of the same call type. Calls of the same type, joined by audible inhaled elements (or pants) were also counted as single calls. On the other hand, calls of one type that were immediately followed by another call type, and usually joined by an audible inhalation,

Table 1. Descriptions of chimpanzee vocalisation and drum structures and their contexts of occurrence.

Vocalisation name	Acoustic characteristics*	Contexts of production
Bark	<400 ms; 600-2000 Hz; sometimes non-linear phenomena	aggression, travelling, hearing other parties of chimpanzees, encountering chimpanzees from neighbouring communities
Short bark	<170 ms; 400-1500 Hz	hunting colobus monkeys
Tonal bark	tonality: tonal; position of max. F ₀ : early, <0.25, as a proportion of bark length	seeing large snakes
Grunt	40-150 ms; 100-350 Hz; tonality: broad range from quite tonal to highly noisy	feeding, greeting, close contact calls at the start of travel, mild threats
'Aaa' grunt	90-150 ms; 500-700 Hz	feeding
Deep grunt	170-1200 ms; 70-400 Hz	feeding
Hoo	170-1200 ms; 200-700 Hz; highly tonal with clear harmonic structure	feeding, mild fear or surprise such as finding animal carcass or small snake, travelling near nesting time
Hoo grunt	series of hoo, grunts or intermediate forms joined with voiced inhaled elements; 80-200 ms; 200-350 Hz; hoo/grunt elements are generally more tonal than the grunt elements of the pant grunt	nesting, occasionally feeding
Laughter	rapid inhaled and exhaled elements, generally quiet and voiced, grading to non-voiced; 50-100 ms; 80-300 Hz; rate of 4-7 exhaled elements/second	play
Pant	unvoiced, rapid inhaled and exhaled elements; duration and F ₀ fall within the range for pant grunts	occasionally grooming or feeding excitement
Pant grunt	series of grunts joined together by voiced inhaled elements; 30-200 ms; 100-200 Hz; tonality: highly noisy	greeting up the hierarchy

* First two measures listed for each call type are the duration of a single element, followed by the fundamental frequency (unless otherwise stated). Measures are intended as a guideline and are approximate rather than definitive.

Table 1. (Continued).

Pant hoot	comprised of up to four phases: introduction: hoos; build-up: series of hoos interspersed with voiced inhaled elements; climax: screams and sometimes barks; let down: similar to build-up but hoos having decreasing pitch	feeding, travelling, meeting chimpanzees from other parties or other communities
Scream	500-1000 ms; 800-2000 Hz; sometimes non-linear phenomena	receiving aggression, fear, as part of pant hoot and sometimes during copulation
Squeak	shorter and more tonal than screams; 50-250 ms; 800-2000 Hz	when threatened by a dominant
Whimper	highly tonal series of hoo-like calls; 100-700 ms, 250-1300 Hz	begging; by infants and juveniles during weaning or separation from the mother; by young adult males when separated from other males
Drum	pounding of hands and/or feet against large, resonant tree-buttresses; 1-30 beats at 2-13 beats/minute; lowest recordable frequencies <20 Hz (Moebius, unpubl. data)	travelling, display, encounters with chimpanzees from neighbouring communities, occasionally arriving at large food sources

were classified as call combinations. For example, the pant hoot sequence, a species specific call combination found in all chimpanzee populations, can be made up of hoos, screams, barks and drums. The hoos, screams and barks usually follow each other without any audible break. In cases where call types were not joined by audible inhalations, such as grunts followed by hoos, different call types occurring in a single bout of calling were classified as call combinations. The time gap between calls in a single bout is considerably shorter than the time gap between call bouts and can be reliably determined by ear. On randomly examining 50 recorded call bouts, we found that the time gap between calls in a call bout was generally less than one second, and never greater than 1.5 seconds. Single call elements which began as one call type and graded to a different call type within the same call element, for example a call starting as a scream and ending as a bark, were not included as call combinations and were also excluded from the analysis.

Analysis of contextual correlates of calls and call combinations

We first tested whether call types occurred in particular contexts more often than expected, using one sample *t* tests (see Table 2 for context definitions).

Table 2. Definitions and activity budgets of contexts and behavioural interactions used to calculate expected values.

Context	Definition	% of total activity budget
Food	Arriving at, collecting or eating food	38%
Travel	Travelling or short pauses for listening during travelling	30%
Response (food)	Within five minutes of hearing chimpanzees from another party, whilst feeding	8%
Response (travel)	Within five minutes of hearing chimpanzees from another party, whilst travelling	9%
Meet (food)	Within three minutes of joining chimpanzees from another party, at a food site	3%
Meet (travel)	Within three minutes of joining chimpanzees from another party, whilst travelling	3%
Neighbours	Within 30 minutes of hearing chimpanzees from a neighbouring community	1%
Nest	Looking for, climbing up to, building or sitting in a nest	3%
Hunt	Hunting or watching others hunting monkeys	0.2%
Alarm	Within 60 minutes of any non-chimpanzee related context that is cause for a alarm, such as seeing a snake or leopard, hearing a leopard or the alarm calls of other primate species	0.1%
Sex	Within 30 seconds of a sexual interaction such as a solicitation, present, or copulation	0.7%
Behavioural interaction		% of total interactions
Aggression/Display	Aggression interaction against another chimpanzees such as attacking, displaying against or arm waving at another individual	12.5%
Receive aggression	Being the receiver of aggressive interactions described above	12.5%
Greeting	Submissive behaviour, such as crouching, bobbing, hesitant approach – also approach and fast approach to within one metre – accompanied by pant grunt, grunt or pant vocalisations	37.5%
Other	All other interactions, such as begging for food, soliciting grooming, grooming, pass other, other approach or pass, hand reach and embrace	37.5%

Expected values for each context, used in Table 7, were calculated according to each contextual definition. The number of minutes chimpanzees engaged in each particular context were made into percentages relative to the total activity budget of all focal follows. Expected values for each behavioural interaction were calculated by dividing the number of each interaction type by the total number of interactions occurring during all focal follows. All contexts were mutually exclusive. The time designated to contexts such as 'meet' and 'alarm' was allocated according to the time period chimpanzees commonly continue to react to each respective event.

Expected values for each context were calculated from the percentage of time chimpanzees spent engaged in each activity. Since activity budgets for adult chimpanzees in Tai do not differ significantly, we have calculated the activity budget across all chimpanzees, using the same time period during which the behavioural data was collected (see Table 2 for calculation of expected values). The data used in the *t* tests were the percentage of a particular call type used in each context for each chimpanzee. The percentages were tested against the expected value of each context. Call types were collapsed into broad categories, for example all grunt types were simply grouped as 'grunts', unless otherwise stated. 'Laugh' was excluded because of its small sample size. We analysed call types where a context or interaction could be clearly attributed. This included all occurrences of less frequently occurring call types. However, for common call types (those with >400 occurrences) a representative distribution of single calls was analysed (taken from a randomly selected 50% of the total number of full day focal follows). In addition to conducting *t* tests, we noted when more than 80% of a call type occurred in a particular context.

Secondly, we tested whether call types were produced in similar proportions in particular contexts, when used in combination with other calls, compared with when produced alone, using paired *t* tests. For this we used the percentage of a call type that occurred in a particular context. As the sample size for some call combinations was small, giving a low statistical power compared to the single calls, we tested whether call combinations occurred in a particular context more than, and not less than, the component calls.

To limit multiple testing we ran one sample *t* tests only when there was at least five percent more calls or drums in a particular context compared with the expected value. We ran paired *t* tests only when there was at least 20 percent more call combinations in a particular context compared with the percentage of single calls. We then corrected for multiple testing using a modified Bonferroni procedure across the *t* tests conducted on each call type (Hochberg, 1988). Although results of all tests were considered significant if $p < 0.05$, because of low statistical power for some call types we have discussed values of $p < 0.1$ after correcting for multiple testing.

To test whether call combinations were likely to occur in a particular order we conducted paired *t* tests on call combinations and combinations with the reverse order respectively, such as pant hoot followed by grunt versus grunt followed by pant hoot.

Results

Distributions of single and combined calls

51% of all calls were produced singularly whereas 49% of calls were as combinations (Table 3), with spectrograms of the most commonly produced shown in Figure 1. Four call types, namely screams, pant hoots, drums and whimpers, were produced more often in combination with other calls than as single calls (Table 3). This was largely because the first three calls together

Table 3. Number of vocalisations and drums occurring alone and in combination with other vocalisation types.

Signal types	Occurring singularly	Occurring in combination
Bark	320	185
Short bark	48	8
Tonal bark	30	11
Grunt	581	156
Deep grunt	400	56
Aaa grunt	724	97
Hoo grunt	146	13
Hoo	872	143
Laugh	18	–
Pant grunt	963	162
Pant hoot [#]	456	1496
Pant	126	46
Scream	286	1381
Squeak	31	5
Whimper	13	37
Drum	63	1101
Total signals produced*	5077	4899
Total number of signal episodes**	5077	1978
% of all signals produced*	51%	49%
% of all signal episodes**	72%	28%

*where a signal combination is counted once for each component signal; **one episode = the production of single or repeated type of signal or signal combination; [#]refers to the 'hoo' section of a pant hoot sequence, normally termed the introduction and build-up phases (Marler & Hobbett, 1975).

made up one of the most commonly produced of all calls, the pant hoot and drum sequence (Figure 1). Only one (laugh) of the 16 call types never occurred in a combination.

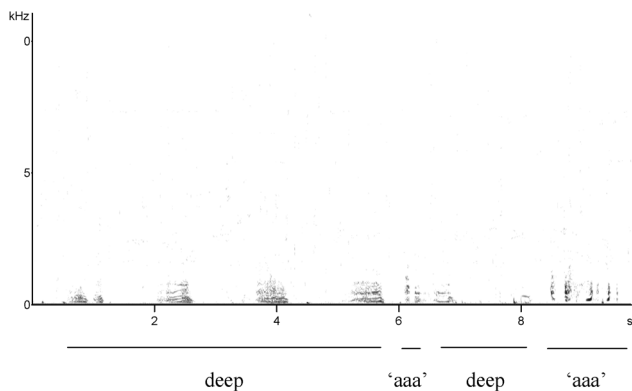
It is evident from Table 4 that the distribution of actual call combinations compared to possible call combinations was non-random. There were a total of 88 different signal combinations, which is 41% of all 214 possible combinations. 12 different combinations were produced more than 20 times whereas 56 were produced fewer than five times.

The call order of six call combinations was non-random (Table 4). In 97.5% of all combinations containing a pant hoot, the pant hoot was the first call in the combination. In other combinations the order was less strict. Although significantly more hoo and grunts were produced than grunt and hoo's, 29% of all possible hoo and grunt combinations were produced as grunts and hoo's. In fact seven additional combinations and their reverse orders were each produced at least five times: grunt and bark, grunt and pant, grunt and pant grunt, pant grunt and bark, pant hoot and pant grunt, scream and bark, scream and whimper. However sample sizes were too small to determine whether these combinations were non-randomly produced.

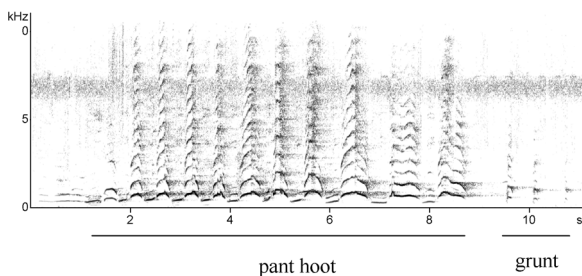
Contextual correlates of single and combined calls

All call types occurred in several contexts, with no call type being exclusively produced in one context. However, single and combined calls showed differences in their frequency of occurrence across contexts. Although all types of single and combined calls were produced in at least three contexts, single calls were generally produced across more contexts. Eight of ten single calls occurred in at least nine contexts whilst this was the case for only two of ten call combinations (Table 5). In addition, only one of ten single calls was mainly produced in one context or behavioural interaction (>80% of all the occurrences of that call type), compared to six of ten different call combinations (Table 7). However, more single call types were produced in certain contexts significantly more than expected, compared with the call combinations (13 and five respectively, Tables 5 & 6 for raw data, & Table 7 for statistical results).

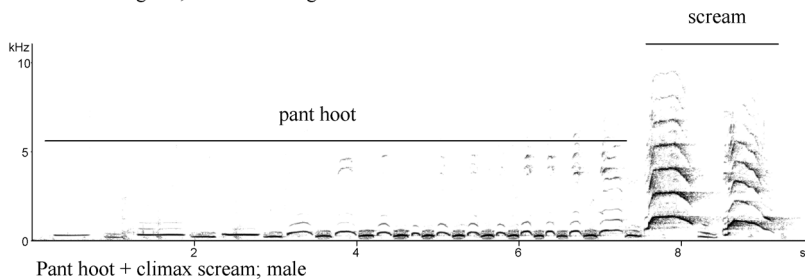
When determining whether similar percentages of call combinations were produced in particular contexts compared to the component calls we found that five of the ten combinations were produced in different contexts com-



Deep grunt + 'aaa' grunt; male eating fruit



Pant hoot + grunt; female arriving at fruit tree



Pant hoot + climax scream; male

Figure 1. Spectrograms of call and drum combinations, shown in Table 8. Vertical axes (Hz); Horizontal axes (sec).

pared to at least one of the component calls (Table 8). For an additional call combination the context specificity was increased relative to the component calls. The call combinations that demonstrated significant contextual changes are shown in Table 8. Overall four different types of change were observed.

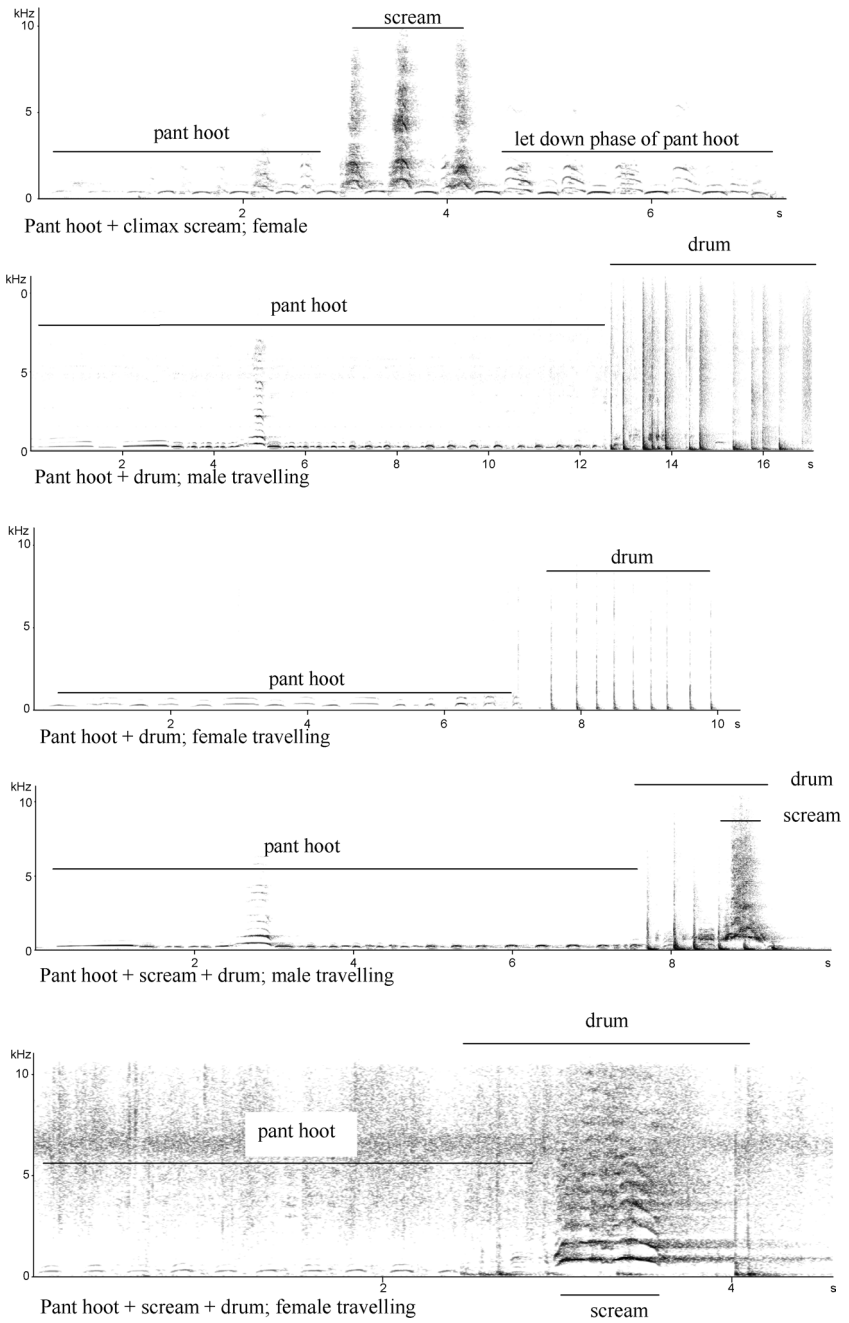


Figure 1. (Continued).

Table 4. Order of signal combinations produced by adult male and female Tai chimpanzees.

Second signal	BA	GR	HO	HG	LA	PN	PG	PH	SM	WP	DR	PH + PG	PH + SM	PH + DR	PH + SM + DR
Bark (BA)	8	2					6	3	8	1					
Grunt (GR)	10	41	24	4	19	26	2	16	1		3				
Hoo (HO)	14	60	-	5	8	4	4	2	3		2	3	2	2	4
Hoo grunt (HG)	2	1	-				1								
Laugh (LA)					-										
Pant (PN)	3	9	1		-	1		1							
Pant grunt (PG)	29	13	7		1	-	5	76			1				
Pant hoot (PH)	5	15				85	-	247	5	160			1		
Scream (SM)	40	4	1		2	2	1	3	1		1				
Whimper (WP)		1			1		3	11							
Drum (DR)	5										-				
PH + PG	5				1	2	3	7			-				
PH + SM	5	5									828		-		
PH + DR	2				2						1			-	
PH + SM + DR	51		2		3			1	1	1	15				-

Bold = combinations that were produced significantly more than the respective reverse order, where $p < 0.05$ using paired t tests. Blanks indicate zeros, which have been removed to improve clarity. Combinations of call subtypes are indicated as values in the diagonal of the matrix, for pairs of the same call type, for example 'grunt + grunt' = 'aaa' grunt + deep 'grunt'.

Table 5. Mean percentages of calls and call combinations per context, across individuals.

Call type	N	Food	Travel	Response (food)	Response (travel)	Meet (food)	Meet (travel)	Neigh-bours	Nest*	Hunt	Alarm	Sex
Call combination												
GRa + GRd	34	91	0	0	0	6	0	0	3	0	0	0
GR + HO	23	47	22	9	0	9	9	0	4	0	0	0
HO + GR	58	51	7	11	0	22	5	0	0	0	2	2
GR + PG	26	42	19	0	0	16	19	0	0	0	0	4
PH** + GR	18	28	0	33	6	22	11	0	0	0	0	0
PH + PG	73	11	8	3	1	37	31	0	8	0	1	0
PH + DM	64	12	50	6	6	8	15	0	0	0	3	0
PH + SM	212	21	22	16	25	7	0	1	5	1	2	0
PH + SM + DM	256	3	62	1	24	1	3	1	0	1	4	0
PH + SM + DM + BA	48	0	61	0	20	0	0	19	0	0	0	0
Single call												
Bark (BA)	311	14	20	7	17	5	7	6	0	8	14	2
Grunt (GR)	490	58	14	2	4	10	4	0	4	2	1	1
Hoo (HO)	370	30	19	7	10	8	6	0	11	1	6	2
Hoo grunt	83	25	5	2	2	4	0	0	62	0	0	0
Pant	73	44	20	0	0	14	16	0	3	1	1	1
Pant grunt (PG)	305	22	40	0	1	12	22	0	2	0	0	1
Pant hoot (PH)	223	18	14	23	19	9	9	0	4	1	3	0
Scream (SM)	229	28	29	0	1	12	11	4	0	4	1	10
Whimper	36	41	30	3	10	3	3	3	0	4	0	3
Drum (DM)	54	2	51	2	13	2	6	20	0	0	2	2

Pooled data of 18 adult male and female chimpanzees. GRa = 'aaa' grunt, GRd = deep grunt. *includes nesting at food site; **includes PH + SM. See Table 2 for context definitions.

Table 6. Mean percentage of call combinations produced during certain behavioural interactions compared with single calls, across individuals. A behavioural interaction is either the signaller directing a behaviour at another or another directing a behaviour at the signaller.

Call type	N	Aggression/ Display	Receive aggression	Greeting food	Meet (food)	Meet (travel)	Travel	Other	Other inter- action	No inter- action
Call combination										
GRa + GRd	34	0	0	0	3	0	0	0	3	94
GR + HO	23	4	0	0	4	9	0	0	0	83
HO + GR	58	0	2	2	2	4	0	2	0	88
GR + PG	26	0	23	31	8	15	19	0	0	4
PH* + GR	18	6	0	0	0	11	0	0	0	83
PH + PG	73	0	5	9	35	28	5	6	3	9
PH + DM	64	39 (21 in travel)	0	0	0	0	0	0	3	57
PH + SM	212	6	0	0	0	0	0	0	0	94
PH + SM + DM	256	5	0	0	0	0	0	0	0	95
PH + SM + DM + BA	48	9	0	0	0	0	0	0	0	91
Single call										
Bark (BA)	311	5	22	0	0	0	1	0	2	70
Grun (GR)	490	2	6	4	2	3	4	0	4	75
Hoo (HO)	370	0	1	2	2	2	0	0	4	89
Hoo grunt	93	0	0	0	0	0	0	0	1	99
Pant	73	0	4	11	3	1	8	0	18	56
Pant grunt (PG)	305	0	13	18	10	21	31	1	3	3
Pant hoot (PH)	223	7	1	1	2	2	1	1	4	81
Scream (SM)	229	2	53	1	2	4	3	0	7	33
Whimper	36	3	14	0	0	0	0	0	22	61
Drum (DM)	54	71 (54 in travel)	0	0	0	0	0	0	0	29

Pooled data of 18 adult male and female chimpanzees. GRa = 'aaa' grunt, GRd = deep grunt. See Table 2 for definitions of behavioural interactions.

Table 7. Contexts and behavioural interactions in which calls were produced more than expected*, after Hochberg-Bonferroni correction.

Call type	$p < 0.01$	$p < 0.05$	>80% of total call type**
Call combination			
GRa + GRd†			Food
GR + HO			Food (food + response + meet)
HO + GR			Food (food + response + meet)
GR + PG			Food (food + response + meet)
PH† + GR		Food (response + meet)	Greeting
PH + PG	Meet (food)	Meet (travel)	
PH + TM			
PH + SM	Response (food + travel)		Travel (travel + response)
PH + SM + TM	Travel		Travel (travel + response)
PH + SM + TM + BA			
Single calls			
Bark (BA)	Hunt, alarm		
Grunt (GR)	Food	Response (travel)	
Hoo (HO)		Alarm	
Hoo grunt	Nest		
Pant			
Pant grunt (PG)	Meet (travel), greeting		Greeting
Pant hoot (PH)		Response (food + travel)	
Scream (SM)	Receive aggression	Sex	
Whimper			
Drum (DM)		Travel, aggression	

* one sample t tests; ** not necessarily produced more than expected, probably because of low statistical power; † includes PH + SM. () = contexts calculated together. GRa = 'aaa' grunt, GRd = deep grunt.

Table 8. Significant contextual changes in the production of call combinations compared with the component calls^a.

Component call	Contexts where component calls occurred more than expected	Call combination	Contexts in which call combinations occurred more than component calls	Classification of call combinations (see table legend)
'Aaa' grunt (GRa) Deep grunt (GRd)	Food Food	GRa + GRd	Food	4
Pant hoot (PH) Drum (DM)	Response in food and travel Travel, aggression	PH + DM	Travel (Aggression)	1
Pant hoot Grunt	Response in food and travel Food	PH + GR	(Response at food)	2
Pant hoot Pant grunt (PG)	Response in food and travel Greet, Meet in travel	PH + PG	Greet (Meet at food & travel)	1, 3
Pant hoot Scream (SM)	Response in food and travel Receive aggression, sex	PH + SM	Response at food (Response in travel)	1
Pant hoot Scream Drum	Response in food and travel Receive aggression, sex Travel, aggression	PH + SM + DM	Travel	1

^a paired *t* tests; contexts without brackets: $p < 0.05$ and () $p < 0.1$ after Hochberg-Bonferroni correction; = call combination is not produced significantly more in any context than the component call. Relative to the component calls, call combinations were produced (1) in the same contexts as only one of the component calls (2) in the sum of the contexts of the component calls (3) in a similar, related context to each of the component calls (4) more specifically in the same context than either of the component calls (numbering is in keeping with that in the discussion).

First, call combinations occurred in the contexts expected for only one of the component calls (Table 8). Pant hoot followed by drums, for example, occurred more in travel and aggression contexts than pant hoots alone, travel and aggression being the two contexts which elicited more drums than expected. Second, pant hoot and grunts were produced in the sum of the contexts of the component calls (Table 8). Pant hoots were produced more than expected in 'responses during feeding and travelling', whilst grunts were produced more than expected in food contexts. Pant hoot and grunts were produced more in 'responses and meeting at food' than expected and in more 'responses at food' than grunts. Thus pant hoot and grunt is produced in the response context associated with pant hoots, but only during feeding, the context associated with grunts. Third, pant hoot and pant grunt combinations were produced more than either of the component calls in a different but related context — 'meeting at food' (Table 8). Fourth, 'aaa' grunt and deep grunt, a combination of two different grunt types, was produced significantly more in food contexts than single grunts, even though single grunts were produced significantly more in food contexts than expected.

The only combination in the analysis for which it was possible to test its reverse pair, hoo and grunts and grunts and hoos, did not show any significant differences, although Table 5 shows that the distribution of calls across contexts is not the same. Although both occurred in food contexts, grunt and hoos occurred more in travel whilst hoo and grunts occurred more in 'meeting at food'. Unfortunately, the small sample sizes of other call combinations and their reverse pairs were too small to be included in the analysis.

Discussion

Almost half of all vocalisations produced by the Tai chimpanzees occurred in combination with other vocalisations or with drums. The combinations were a non-random selection of possible combinations, some of which occurred in a specific order. Single calls and call combinations were produced in specific contexts. The contexts in which several combinations were produced differed from the contexts of at least one of the component calls. The contexts in which the combinations were produced varied from the component calls in five different ways, three of which have not, to our knowledge, been described for other animal species. This analysis clearly shows that call combinations are an important aspect of chimpanzee communication.

Half of all vocalisations and drums were produced as combinations compared to 38% of all calls in wedge-capped capuchins, a species known for their extensive combining of calls (Robinson, 1984). While most of these were the more stereotyped pant hooting sequences, 19% were combinations from a range of call types and contexts. The latter is likely to be conservative estimate in chimpanzees, as calls were categorised by ear rather than spectrographically. Thus, more subtle call combinations or rapid call changes may have been missed. Clearly, call combinations constitute a substantial proportion of the vocal repertoire of chimpanzees.

Call combinations were non-randomly produced, a finding also shown for new world monkeys (cotton-top tamarins: Cleveland & Snowdon, 1982; wedge-capped capuchins: Robinson, 1984). While few combination types occurred frequently (more than 50 times), more than half of the combination types were rarely produced, less than 5 times in total. This suggests that although the observation time was probably not long enough to observe all possible combinations, a fluid, rather than a rigid, stereotyped, combination system seems to exist, whereby calls can be combined as contexts arise that require them.

As with other primates, some call combinations were more likely to occur in a specific order rather than the reverse order. In cotton-top tamarins, for example, chirps were always followed by whistles (Cleveland & Snowdon, 1982). In titi monkeys pants followed chirrups but chirrups never followed pants (Robinson, 1979). Using a playback experiment, Robinson (1979) showed that titi monkeys can discriminate variations in the order of call combinations, as has also been shown for gibbons (Mitani & Marler, 1989), golden-winged warblers (Ficken & Ficken, 1973) and the European robin (Bremond, 1968).

However, as pointed out by Robinson (1979), it has not yet been demonstrated in a species other than humans and captive chimpanzees (e.g., Gardner & Gardner, 1969; Premack, 1971), that changing the call order actually constitutes a difference in the information which is extracted from calls by listeners, for example 'chimpanzee hunt' versus 'hunt chimpanzee'. We found that eight call combination types and their reverse orders were produced. Further research should test whether call order affects the information conveyed to chimpanzees.

Single call types were produced broadly, across several contexts. Screams, like barks, occurred more than expected in at least two contexts. After using

detailed acoustic analysis with barks we know that two of these contexts ('alarm' and 'hunt') elicit specific bark types that are rarely produced in other contexts (Crockford & Boesch, 2003). Detailed acoustic analysis of screams may also reveal context specific call types.

Only one single call was predominantly produced in a single context. In contrast, more than half of the different call combinations were context specific, each being mainly produced in a single context. One explanation for this is that the act of combining calls refined the likelihood of a particular combination being produced in a particular context.

The effect of combining calls altered their contexts of production in five ways, suggestive of five possible functions that call combinations may have relative to the component calls. Two of these call combinations have already been documented for other species and are as follows. Some pant hoot and pant grunts were produced in a context related to, but not the same, as contexts of the component calls. Similarly, cotton-top tamarins (Cleveland & Snowdon, 1982) and wedge-capped capuchins (Robinson, 1984) call combinations have been described as occurring in contexts intermediary to those of the component calls, constituting an early form of lexical syntax. The 'aaa' grunt and deep grunt combinations would seem to have a message intensification function, as described for wolves (Schassburger, 1993). Again, this constitutes an early form of lexical syntax.

Three remaining putative functions of the call combinations found in chimpanzees, to our knowledge have not yet been described for other animal species. First, the pant hoot and pant grunt combination, a longer range and a shorter range call respectively, may convey information simultaneously to different audiences. The combination is produced exclusively by females in Tai, specifically while greeting males during meeting contexts (Tables 3 & 4). The pant hoot usually starts as the female joins the new party whilst the pant grunt part only begins during the final approach to the male. As such, the pant hoot part may announce her arrival to the party as a whole and the pant grunt act as a greeting, exclusively directed at the male. Other combinations, not included in the analysis for reasons of sample size, may function similarly.

Second, the pant hoot and grunt combinations, produced in the sum of the contexts of the component calls, might convey information about co-occurring, rather than intermediary, contexts, such that both contexts are combined in a purely additive fashion. Thus, two pieces of information can

be decoded simultaneously, rather than just one. This would fit the description of lexical syntax (Marler, 1977), however not as a form of contextual modification (Robinson, 1984).

A third, possibly related, function may explain why pant hoots are mainly combined with all other long distance calls and drums, but rarely with short distance calls. The main context of production of pant hoots was in response to hearing chimpanzees in another party. Three of five of the combination types with a pant hoot were produced in other contexts, however, as if the pant hoot 'loses' its context of production (pant hoot and drum, pant hoot and scream and drum, pant hoot and pant grunt). It might be that the function of the pant hoot changes, or that we have wrongly inferred the function of single pant hoots from their contexts of production. Pant hoots are known to encode individual and community differences (Marler & Hobbett, 1975; Crockford et al., 2004). Anecdotally, they are the easiest vocalisation by which researchers can identify out-of-sight chimpanzees, although encoding of individuality in other chimpanzee calls has not yet been examined. In addition, although pant hoots are combined with a range of other calls and drums, they are produced almost exclusively at the beginning of combinations. Furthermore, barks produced in combination with drums are produced specifically in either travel or neighbour encounter contexts (Crockford & Boesch, 2003). Barks and drums are also often combined with pant hoots (Table 5).

We hypothesise then that pant hoots act as signature calls for signallers, which can be combined with context information in the calls or drums which follow. If this is the case, this may represent a primitive form of 'agent' combined with 'context'. Again this suggests an additive function, where two pieces of information can be decoded instead of one, such that the complexity of information available for decoding is increased.

Finally, one function discussed in the literature, was not found in chimpanzees. This is where combined calls were produced in completely different contexts to those of the component calls, such as in gibbon song (Mitani & Marler, 1989), in other words constituting an early form of phonological syntax (Marler, 1977). The evidence in this study goes against Marler (1977)'s suggestion, that chimpanzees' apparently stereotyped pant hoot sequences demonstrate a primitive form of phonological syntax.

Several of the call combinations that we have found in chimpanzees fit the broad descriptions so far offered for lexical syntax (Marler, 1977; Robinson,

1984). The term lexical syntax may be appropriate for human language, however, it is clearly too broad a term to discriminate between the different types of combinations that we have so far seen in chimpanzees. Careful testing using playback experiments, such as those conducted by Zuberbühler (2002), of each component signal and of the call combination, is required to determine what information is really conveyed by single calls, and how this changes when calls are used in combination. Only then can we begin to compare apparent forms of lexical syntax found in animal communication with those found in human languages, and so determine if roots of human language or language abilities exist in animal communication.

Call combinations clearly make up a substantial part of the chimpanzee repertoire. By analysing the contexts in which call combinations were produced compared with the information conveyed by each call singularly we have highlighted five possible functions of call combinations. Two resembled those described for other species, whilst three represent novel functions. Two of the three may have an additive function, such that two pieces of information can be conveyed simultaneously, increasing message complexity. Although the functions of these call combinations remain to be tested, it seems likely in chimpanzees that call combinations serve several functions, all of which enable listeners to extract more precise information about the signaller or the current situation of the signaller. Since so many different call combinations were used, call combinations must provide a rich source of information. It seems highly likely that we are and will continue to underestimate the types and complexity of information conveyed in chimpanzee calls until the information content of call combinations is tested. In addition, such an analysis may be crucial for determining whether or not the roots of human language date back to when humans last shared a common ancestor with chimpanzees, some 4-6 million years ago.

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