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## Vocal responsiveness in male wild chimpanzees: implications for the evolution of language

Several captive chimpanzees and bonobos have learned to use symbols and to comprehend syntax. Thus, compared with other nonhumans, these animals appear to have unusual cognitive powers that can be recruited for communicative behavior. This raises the possibility that wild chimpanzee vocal communication is more complex than heretofore demonstrated. To examine this possibility, I investigated whether wild chimpanzee vocal exchanges exhibit uniquely human conversational attributes. The results indicate that wild chimpanzees vocalize at low rates, tend not to respond to calls that they hear, and, when they do respond, tend to give calls that are similar to the ones they have heard. Thus, chimpanzee vocal interactions resemble those of other primate species, and show no special similarity to human conversations. The results support the view that we need to explore cognitive and social continuities and discontinuities with nonhuman primates to understand the origin and evolution of language, but also emphasize the need for fine-grained analyses of wild chimpanzee vocal interactions.

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### Introduction

Several captive chimpanzees have learned to use symbols (*Pan troglodytes* and *P. paniscus*) and to comprehend syntax (in the sense of being sensitive to word order in spoken English: *P. paniscus*), possibly to the degree manifested in normal 1- to 2-year-old children (Savage-Rumbaugh, 1986; Kako, 1999). In the process of acquiring these skills, the animals also improved their ability to take turns during communicative interactions. Thus, these chimpanzees achieved some proficiency with both structural and interactional aspects of language. Since language-like abilities are exceptionally difficult for nonhumans to learn, even limited success at teaching language skills to chimpanzees suggests the possibility that communication among wild chimpanzees may be more complex than previously thought (Savage-Rumbaugh & Rumbaugh,

1993; Savage-Rumbaugh & Lewin, 1994). Evidence of language-like communicative complexity in wild apes would constitute important evidence for linguistic preadaptation in these animals, and, therefore, would be useful for developing hypotheses about the origins of language in humans.

Observations under experimental, naturalistic captive, and wild conditions indicate that chimpanzees can transmit and receive a great deal of information about future behaviors and about their social and physical environment through postures and gestures (Menzel, 1971; de Waal, 1982; Goodall, 1986). However, there is no indication that the signals involved are symbolically or syntactically structured. On the other hand, observers typically comment on the apparent complexity of wild chimpanzee vocal displays. Chimpanzee vocalizations are highly graded with many variants used in a wide range of contexts, vocal sequences can

be long and involve many call types, and extended vocal exchanges between individuals out of visual contact are common (Goodall, 1968, 1986; Marler, 1969, 1976; Mitani & Nishida, 1993). This raises the possibility that chimpanzee vocal interactions may exhibit conversational characteristics (Boehm, 1992).

In human conversation, individuals take turns producing language (Sacks *et al.*, 1974). Drawing on the vast reservoir of possible utterances afforded by the syntactical nature of language, speakers are routinely able to produce novel and meaningful combinations of speech sounds in response to one another. Thus, human conversation is typically characterized by the orderly exchange of acoustically distinct sounds, although partial repetition between speakers may foster conversational cohesion (Tannen, 1987). By contrast, although simple vocal exchanges involving distinct calls have been documented in some primate species (Snowdon & Cleveland, 1984; Biben *et al.*, 1986), the calls involved are extremely similar acoustically. Whether the seemingly variable vocal displays of chimpanzees represent conversation-like exchanges of distinct acoustic signals, or, as in other nonhuman primate species, they are primarily repetitive, is unknown.

The goal of the study reported here was to investigate how wild chimpanzees respond vocally to calls they hear. To date, there exist few quantitative data on how often chimpanzees respond to particular calls (Mitani & Nishida, 1993, for pant hoots only), or on which calls they use in counter-calling and chorusing bouts (Arcadi, 1996). This research, which builds on an earlier analysis of the tendency for chimpanzees to "pant hoot" when other individuals are pant hooting (Arcadi, 1996), explores whether wild chimpanzee vocal interactions in general have conversational attributes. The results suggest that chimpanzee vocal interactions are no more complex than those

reported in other primate species. This in turn implies that the specific structures of chimpanzee calling bouts will be no more informative than those of other primate species for understanding the evolution of language. I suggest that if unique behavioral preadaptations for language are present in chimpanzees, they will more likely be found in the neurological control of vocal production, and in the organization of chimpanzee social interactions in general.

## Methods

### *Study site and animals*

Observations were made from 1 December 1996 to 22 January 1997 in the Kanyawara study area in the Kibale National Park in western Uganda. Kibale is a small, mid-altitude evergreen rain forest (766 km<sup>2</sup>, maximum altitude 1590 m, mean annual rainfall 1570 mm: Butynski, 1990) surrounded by subsistence agriculture. The Kanyawara chimpanzees were first habituated from 1983–1985 by G. Isabirye-Basuta (Isabirye-Basuta, 1989), and have been under continuous observation since 1987 (see Chapman & Wrangham, 1993, for details regarding the study site and animals). At the time of this study, the Kanyawara community included ten adult males, eight central adult females, an additional nine peripheral mothers intermittently observed in the northern and southern parts of the community range, and ten adolescent males. With the exception of some northern and southern mothers, the community was fully habituated and could be observed at close range (<5 m). The Kanyawara chimpanzees have never been provisioned, although they occasionally raid crops when fruit availability in the forest is low.

### *Sampling protocol*

The vocal behavior of specific individuals was monitored using focal-animal sampling

(Altmann, 1974). Individual animals were observed uninterrupted for ten minutes (10-min samples, or TMS) in a rotation schedule predetermined each morning as follows. Sampling began as soon as individuals came into view. Individuals observed the least frequently to date were chosen before individuals more commonly seen. A sequence was thus established in reverse order of how often the individuals had so far been sampled. This sequence was maintained throughout the rest of the day, with the following exceptions. If an individual was not clearly in view when it was his/her turn, it was skipped until it came into view. In addition, chimpanzees periodically leave and join subgroups. New arrivals were integrated into the rotation as soon as they were clearly visible and after the current TMS was completed. Individuals were not sampled more than once every 30 min.

Out of a total of 132.5 contact hours on 33 days, call data were collected during 97.8 hr of focal observation time, distributed as follows: 61.25 hr on adult males ( $\bar{X}=6.8$ , S.D.=2.9,  $n=9$ ), 22.1 hr on subadult males ( $\bar{X}=9.0$ , S.D.=1.8,  $n=2$ ); 11.9 hr on adult females ( $\bar{X}=2.2$ , S.D.=3.1,  $n=9$ ) and 2.0 hr on subadult females ( $n=1$ ).

#### *Data collection*

I noted on checksheets all calls that I could hear during each TMS, including both those of the target and those heard from other individuals. Calls given by non-targets were divided between those from individuals within the target's subgroup and those from individuals in other subgroups. Subgroup membership was operationally defined as all individuals within 50 m of one another. Since a grid of trails spaced 50 m apart is maintained throughout most of the study area, it was relatively easy for an accompanying field assistant quickly to monitor the area surrounding parties that were not tightly clumped, making party

composition determinations reliable despite areas of dense vegetation.

The study period coincided with the ripening of a large crop of *Mimusops bagshawei* fruits, a preferred food of the Kanyawara chimpanzees, on a loose cluster of trees localized in a roughly  $\frac{1}{2}$ -km<sup>2</sup> sector of the study area. During this period I observed daily up to 25 chimpanzees variably dispersed into smaller subgroups in the same general area of the forest. Loud calling was common between these parties, and call exchanges occurred between groups estimated to be separated by as much as 500 m.

Vocalizations were assigned to 16 categories during field observations (Clark, 1993; Table 1, left column). The categories were based primarily on Marler's (1976; Marler & Tenaza, 1977) catalog of chimpanzee vocalizations. Discrimination in the field was based on reference to a tape recording of Gombe chimpanzee vocalizations from a film soundtrack (Marler & Lawick-Goodall, 1971), and to Goodall's (1968, 1986) written descriptions of chimpanzee vocalizations and the contexts in which they occur. Different vocalization types uttered in succession were scored separately.

The following differences from Marler, which were also observed in my previous analyses (Clark, 1993; Clark & Wrangham, 1993; Arcadi, 1996), are shown in Table 1: (1) I scored hoots separately from pant hoots if no climax phase occurred; (2) I distinguished "whimper hoots" (Marler & Hobbett, 1975) from pant hoots. Whimper hoots are patterned like pant hoots, but they are higher pitched and, like the whimper, are characterized by irregular increases and decreases in pitch within call phrases (Arcadi, 1996); (3) as discussed below, I lumped for analysis a number of calls that were often difficult to distinguish in the field, i.e., (a) all soft food calls, and (b) all non-food-related grunts and pants; (4) following Goodall (1986), I distinguished hoots

Table 1 Vocalization categories used in this study (following Clark, 1993), compared with Marler &amp; Tenaza (1977) and Goodall (1986)

This study	Marler & Tenaza (1977)	Goodall (1986)	Context (Goodall, 1986)*
Pant hoot	Pant hoot	Roar pant hoot Arrival pant hoot Inquiring pant hoot Spontaneous pant hoot (With "pant hoots")	Charges, stranger contact, social excitement Arrival at good food source, joining others During travel, on high ridges During peaceful feeding, resting
Hoot†	(With "pant hoots")		
Bark	Bark	Bark	Social excitement, especially females
Waa-bark	Waa-bark	Waa-bark	Agonistic contexts, often by bystanders
Cough	Cough	Cough (or soft bark)	Mild threat given to lower ranking individuals
Hoo	Whimper	Hoo Huu	Contact call, beg, especially mothers and infants Surprise, mild anxiety to unfamiliar objects
Food grunt	Grunt Rough grunt	Food grunt Food aaa	Begin calm feeding on preferred food Excited feeding, approaching preferred food
Copulation scream	(With "scream")	Copulation scream	Females during copulation
Whimper	Whimper	Whimper	Distress, especially infants (series of "hoots")
Squeak	Squeak	Squeak	Response to threat by dominant individual
Scream	Scream	Victim scream Tantrum scream SOS scream (Copulation scream)	While being attacked Weaning conflict, post-aggression frustration Appeal for help after attack
Grunt	Pant-grunt	Crying Pant-grunt Pant-bark Pant-scream Pant Soft grunt Extended grunt	Infant/juvenile, combine whimper and tantrum scream Up hierarchy, reunions, social excitement Up hierarchy, reunions, social excitement Up hierarchy, reunions, social excitement Greeting, grooming During foraging or traveling Resting
Copulation pant	(With "pant")	Copulation panting	Males during copulation
Nest grunt‡	(With "grunt")	Nest grunt	Looking for nest site, make nest, settle in nest
Laughter‡	Laughter	Laughter	During play
Wraah‡	Wraah	Wraah	Alarm at dangerous creatures, bizarre behavior

\*All of Goodall's (1986) contexts apply to the lumped categories used by Marler & Tenaza (1977) and myself.

†I treated "hoots" and "pant hoots" separately, since they are easily distinguished (hoots have no climax phase), but they can be readily combined for comparative purposes. See text for details about lumping categories. In general, my lumping does not reflect disbelief in a narrower category, but rather my inability to systematically discriminate intergraded calls under field conditions.

‡"Nest grunt", "laughter", and "wraah" were not observed during focal observations.

and whimpers. A whimper is a series of hoos, and therefore Marler & Tenaza (1977) lumped them all as whimpers; and (5) also following Goodall (1986), I distinguished male and female copulation calls because of their context specificity. I also noted the occurrence of buttress drumming, a nonvocal long-distance signal that is often associated with pant hoots, is typically produced during travel, and appears to be individually distinctive (Arcadi *et al.*, 1998).

I used Marler's (1976) catalog, as opposed to Goodall's (1986) more extensive 32-call catalog (compared in Table 1), because it is difficult to distinguish Goodall's finely discriminated, related call types under Kibale field conditions. Therefore, acoustically similar call variants identified by Goodall (1986) that commonly intergraded with one another were lumped together, even though the extreme forms could be distinguished. For example, pants, grunts, and the combined pant-grunts are relatively easy to distinguish, and I scored them separately in the field. However, a submissive individual will commonly employ all three in an extended vocalization sequence, grading from one to the next without pause or obvious order, and merging type forms into ambiguous amalgamations. Consequently, analyzing such frequently intergraded calls separately would have overestimated my ability to distinguish them reliably under field conditions. Although lumping vocalization categories undoubtedly masked some of the complexity of chimpanzee vocal behavior, broad patterns of response were most probably preserved. The use of playback experiments will be necessary ultimately to elucidate any subtleties that may exist within groups of acoustically similar calls.

Successive utterances of the same vocalization type (e.g., a sequence of screams without pause) were scored only once, following Marler (1976). If a pause of at least one minute occurred, the vocalization was

scored again. Two compound calls, the pant hoot (which includes hoos, hoots, and scream-like elements) and the whimper (which comprises a series of hoos), were scored as single vocalization types (i.e., their components were not scored). When more than two non-target individuals were calling simultaneously, I recorded the bout as a chorus.

Finally, although it is possible that some soft calls may have gone undetected during data collection, this was unlikely to have been a significant source of error. I used only focal-animal data from well-observed targets that were never more than 20 m away, and generally much closer (5 m). Most soft vocalizations are easily audible in this range. In addition, the most likely context for vocalizations to go undetected is during periods of group excitement when many individuals are vocalizing and moving about. Yet it is in these very contexts that individuals tend to vocalize loudly.

#### *Analysis*

I calculated the following from individual call data collected during focal-animal sampling:

(1) *The overall rate (calls/hour) at which each individual vocalized, and mean vocalization rates for all individuals and for each age/sex class.* Individuals were assigned to age/sex classes based on known ages and observed maturational state, following Goodall's (1986) criteria.

(2) *The percentage of all calls an individual gave that were represented by each call type.* In conjunction with (1), these data were used to determine whether adults and subadults used the different call types with the same frequency.

(3) *The rate at which individuals vocalized when other calls were or were not heard during the focal's TMS.* These data indicate whether individuals were more likely to call when other individuals were calling, although they

do not specify whether or not the focal's calls were responses to particular calls heard. In addition, because the data were collected during a rotating TMS schedule, I was unable to conduct a matched comparison of individual calling rates following different acoustic conditions, e.g., rates after periods of quiet *vs.* rates after periods when calling was heard. Thus, the data represent the tendency of calls to clump in time.

(4) *The percentage of calls individuals gave that were in "response" to other calls, and the percentage of calls that individuals heard to which they "responded"*. A call was considered a "response" if it was given while another individual was still vocalizing, or within 5 seconds of the termination of another individual's call (also termed "vocal coordination": Itani, 1963).

I chose this response threshold interval in an attempt to simultaneously maximize the inclusion of real responses while minimizing misclassifications that would result from longer intervals. That is, although a shorter interval, such as 1 sec (used by Harcourt *et al.*, 1986, for gorilla close calls), would minimize the inclusion of calls elicited by other stimuli, it would also miss many probable responses. Whereas within-group contact calls are accompanied by a rich communicative context that makes it possible for individuals to respond nearly instantaneously, interparty calls in chimpanzees appear to require more processing time. For example, a chimpanzee may stop feeding or grooming and gaze in the direction of distant calls, wait a few seconds, vocalize, and then resume feeding or grooming.

By the same token, a longer interval, such as 1 min, would unquestionably capture many calls uttered in response to subsequent vocalizations. Interparty calling exchanges in chimpanzees can persist for 15 min or more, and include many individuals and many call types. These long exchanges, however, are often punctuated by brief periods of silence (<1 min). Thus, a

1-min interval would often overlap with more than one call stimulus.

Finally, there was no way in this study to discriminate reliably between calls uttered as responses and those representing chorusing behavior, since both could in principle be initiated at any time throughout the duration of the initial call. The conceptual distinction between the two is that responses are directed at the first caller, whereas choruses are directed, along with the first call, toward a third party or parties. Moreover, I was unable to control for the possibility that callers were vocalizing independently and not responding to, or chorusing with, other callers (Cheney *et al.*, 1996; Rendall *et al.*, 1999). Operationally, therefore, "responses" in this study include any calls that co-occur, within 5 s, with another call. That is, I am quantifying the tendency of calls to be clumped in time, which could result from (1) true responding, (2) independent responsiveness to different external stimuli, or (3) chorusing behavior. The implication of this methodological constraint is that true responses occur even less frequently than reported here (see Discussion).

(5) *The percentage of calls, by type, heard within the target's subgroup only that individuals "responded" to*. These data were used to compare response patterns of adults and subadults.

In addition, the call types were also grouped into two broad functional classes, "submissive" and "nonsubmissive" calls, to determine if individuals were more likely to respond to one class of calls *vs.* the other (Clark, 1993). Squeaks, screams, and pant-grunts are associated with social apprehension or fear (Goodall, 1986; Table 1), and form the basis of the submissive vocalization group. A fourth vocalization, the whimper, frequently intergrades with squeaks and screams, and therefore was also included in the submissive vocalization group. Submissive vocalizations are typically given by

lower ranking individuals during agonistic interactions with higher ranking individuals.

The remaining calls were designated as "nonsubmissive". With the exception of hoos, coughs, and male copulation pants, these vocalizations are loud and are often given during exchanges between individuals out of visual contact. By contrast, the cough is usually directed at a specific individual and occurs in agonistic interactions, but is given by the higher ranking individual (e.g., often when a higher ranking individual supplants a lower ranking one). The hoo is also often directed at specific individuals, for example between mothers and offspring. However, it may be generally broadcast, and may occur in response to distant vocalizations or as part of a vocal exchange. The copulation pant can be heard only in the immediate vicinity of a pair of copulating animals.

In those cases in which two or more individuals in the subgroup were calling simultaneously, the calls heard by the target were designated as either submissive or non-submissive "choruses". I did not include in the analysis calls heard from other subgroups (8% of all calls heard), since it was difficult to determine whether the target was responding to the distant call or to the response calls of other members of its subgroup.

(6) *The percentage of "response" calls that were of the same type as the call heard.* These data offer a comparison to linguistic interactions in which the acoustic structures of responses differ sharply from those of stimuli.

Data for males only are analyzed. When fruit availability is high the size of chimpanzee subgroups increases, and females tend to associate intermittently with males rather than foraging alone (Chapman *et al.*, 1994). Fruits were abundant during the present study, and groups of males with occasional females associated together daily. Therefore, I concentrated my observations

on these mixed parties in which males generally outnumbered females. Females, consequently, were sampled less than males. Although I calculated average hourly call rates for all individuals, only males were sampled enough to permit statistical analysis. A substantially longer study period will be necessary to collect comparative data on females since Kanyawara females rarely vocalize when they are not associating with males (Clark, 1993), and females with offspring spend 60–70% of their time foraging alone (Wrangham *et al.*, 1992).

## Results

(1) *At what rates do individuals produce calls?*

Overall call rates for adult and subadult males were  $2.6 \pm 2.0$  and  $2.8 \pm 0.3$  calls per hour, respectively (mean  $\pm$  s.d.: because there are only two subadult males in the sample no statistical comparison was made). These rates are similar to previously reported rates of 2–4 calls per hour at Kibale and Mahale (Clark, 1993; Mitani, 1996). Higher rates were reported by Marler (1976) at the Gombe feeding station, but these most probably reflected a bias introduced by the presence of large, excited parties during provisioning (Clark, 1993).

(2) *Do adult and subadult males differ in their tendency to produce particular types of calls?*

Consistent with previous reports, although adult and subadult males called at similar rates overall, they emphasized different calls (Marler & Tenaza, 1977; Clark, 1993) (Figure 1). Vocal production by adult males was dominated by pant hoots, hoots, and hoos (74% of calls given). By contrast, vocal production by subadult males was dominated by waa-barks, grunts, and hoos (71% of calls given).

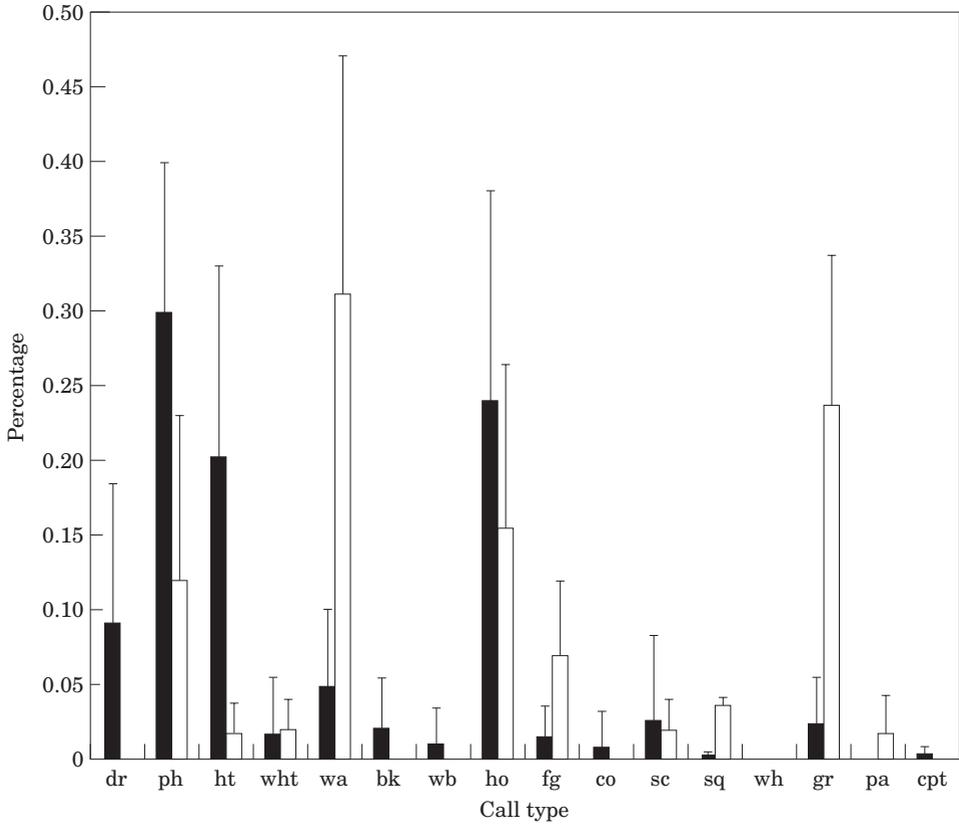


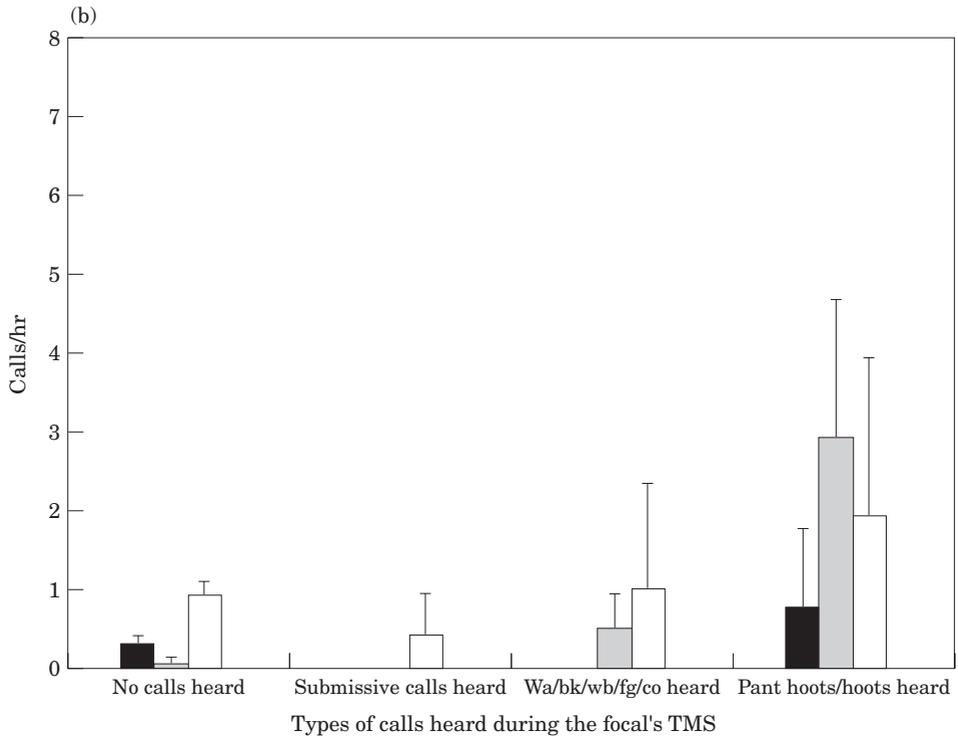
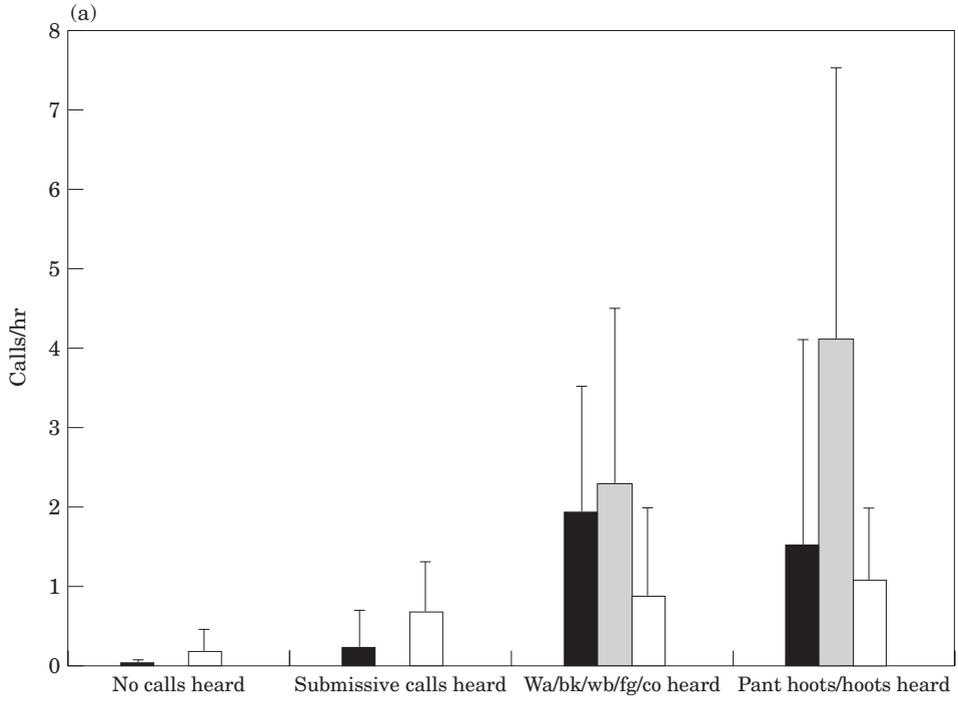
Figure 1. The percentage of an individual's calls that was represented by each call type, averaged across individuals (lines show standard deviations). Solid bars, adult males ( $n=9$ ); open bars, subadult males ( $n=2$ ); dr, buttress drumming; ph, pant hoot; ht, hoot; wht, whimper hoot; wa, waa; bk, bark; wb, waa-bark; ho, hoo; fg, food grunt; co, cough; sc, scream; sq, squeak; wh, whimper; gr, grunt; pa, pant; cpt, copulation pant.

(3) *Do individuals tend to call more often when other calls are audible?*

Adult males produced pant hoots and hoots significantly more often when non-submissive calls (including and not including pant hoots and hoots) were heard during their TMS, compared with when no calls or only submissive calls were heard (Kruskal-Wallis,  $df=3$ ,  $H=19.031$ ,  $P<0.001$ , with a

*posteriori* comparison from Conover, 1980) [Figure 2(a)]. The differences in hooting rates between the two nonsubmissive calling contexts were not significant; similarly, the differences in hooting rates between the no calls *vs.* submissive calls contexts were not significant. Adult males also produced nonsubmissive calls other than pant hoots and hoots significantly more often when

Figure 2. Rates at which adult (a) and subadult (b) males gave calls when other calls were or were not heard during the focal's TMS, averaged across individuals (lines show standard deviations). Solid bars, wa/bk/wb/fg/co given; stippled bars, pant hoots/hoots given; open bars, submissive calls given. For adult males (above), means were calculated from  $n=8$  individuals for no calls and submissive calls heard,  $n=7$  for wa/bk/wb/fg/co heard, and  $n=9$  for pant hoots/hoots heard.  $n=2$  individuals for subadult males. See Figure 1 for call abbreviations.



**Table 2** Calls given by adult and subadult males, either spontaneously or in “response” to calls heard

Calls given and heard by targets	Adult males ( <i>n</i> =9)	Subadult males ( <i>n</i> =2)	Total ( <i>n</i> =11)
<b>Percentage of all calls given that followed a call heard</b>			
Numbers of calls given	164 (18.2 ± 16.2)*	56 (28.0 ± 2.8)	220 (20.0 ± 15.1)
Number of calls that followed a call heard	67 (7.4 ± 5.1)	22 (11.0 ± 1.4)	89 (8.9 ± 4.8)
Percent of all calls given that followed a call heard	41.8% (47.0 ± 25.8)	39.3% (39.2 ± 1.1)	41.2% (46.2 ± 23.5)
<b>Percentage of all calls heard to which targets “responded”</b>			
Numbers of calls heard	576 (64.0 ± 29.7)	139 (69.5 ± 0.7)	715 (65.0 ± 26.6)
Number of calls that followed a call heard	67 (7.4 ± 5.1)	22 (11.0 ± 1.4)	89 (8.9 ± 4.8)
Percent of all calls heard to which targets “responded”	11.6% (11.5 ± 6.1)	15.8% (15.8 ± 1.9)	12.4% (12.2 ± 5.8)
<b>Percentage group calls heard to which targets “responded”</b>			
Calls heard from within group only	467 (51.9 ± 21.8)	106 (53.0 ± 1.4)	573 (52.1 ± 19.5)
Group calls heard to which targets “responded”	49 (5.4 ± 4.4)	8 (4.0 ± 2.8)	57 (5.2 ± 4.1)
Percent group calls heard to which targets “responded”	10.5% (9.4 ± 5.8)	7.5% (7.5 ± 5.1)	9.9% (9.0 ± 5.5)

\*Mean ± S.D.

other non-hoot nonsubmissive calls were heard, compared with when no calls or only submissive calls were heard (Kruskal–Wallis,  $df=3$ ,  $H=10.586$ ,  $P<0.01$ , with a *posteriori* comparison from Conover, 1980). These calls were produced significantly more often when pant hoots and hoots were heard compared with when no calls were heard, but not compared with when submissive calls were heard. There were no significant differences in the rates at which submissive calls were produced in the different contexts (Kruskal–Wallis,  $df=3$ ,  $H=3.978$ ,  $P>0.05$ ).

Rates of nonsubmissive calling by subadult males also appeared to increase when nonsubmissive calls were heard, while rates of submissive calling varied little in the different contexts [Figure 2(b)]. The small number of subadult males precluded statistical comparison.

(4) *Do individuals tend to “respond” to the calls that they hear?*

Although the rate of nonsubmissive calling increased in the presence of other calls, male

chimpanzees nonetheless did not “respond” to the majority of vocalizations that they heard. The mean percentage of calls to which individuals “responded” was 12.2 ± 5.8% for all calls, and 9.0 ± 5.5% for calls from their group ( $n=11$  males; Table 2).

Less than half of the vocalizations that targets did produce followed other calls (46.2 ± 23.5; range: 84% for waas to 0% for most submissive calls;  $n=11$  males) (Table 2). That is, the majority of their calls were given “spontaneously”. The low number of calls per individual prevented a meaningful statistical comparison by call type.

(5) *Do individuals “respond” to some calls more than others?*

Individuals “responded” to nonsubmissive calls significantly more often than they did to submissive calls (all males: paired *t*-test,  $df=21$ ,  $t=11.2$ ,  $P<0.001$ ; adult males only: paired *t*-test,  $df=17$ ,  $t=10.0$ ,  $P<0.001$ , Figure 3). Adult males appeared to

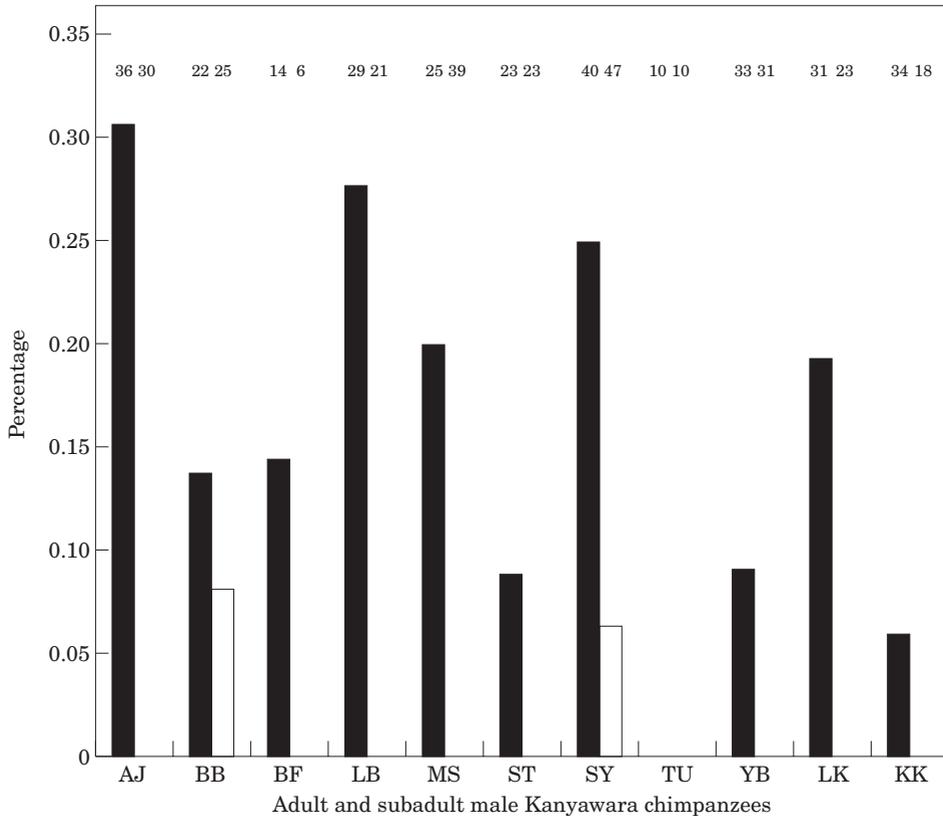


Figure 3. The percentage of (■) nonsubmissive and (□) submissive calls heard to which each individual “responded”. Numbers above bars represent the total number of nonsubmissive and submissive calls each individual heard (i.e., all the calls that were audible to me). LK and KK are the subadult males.

“respond” to a wider range of calls than did subadult males, but the small subadult male sample precluded statistical comparison (Figure 4). In addition, choruses appeared to elicit more “responses” than isolated calls.

(6) *When individuals hear a particular call, with what call are they likely to “respond”?*

The majority of calls produced after hearing another vocalization were of the same type as the call heard (Figure 5). This result is clearest for pant hoots and choruses of non-submissive calls, where sample sizes were largest. The 12 responses to the 15 non-submissive choruses heard consisted of 8 hoots and 4 waa-barks. The data are pooled

because the number of “response” calls for most call types was low, rendering comparisons of means difficult to interpret.

## Discussion

Many animals, including primates, produce vocalizations that are similar to those they have just heard. For example, in some primates mated pairs sing “duets” (sometimes referred to as “antiphonal calling”) and neighbors “countersing”, and in both cases similar calls are uttered in an alternating but precisely timed manner [e.g., gibbon species, *Hylobates* (Tenaza, 1976; Haimoff, 1981; DePutte, 1982; Raemakers & Raemakers, 1984; Mitani, 1985a); titi

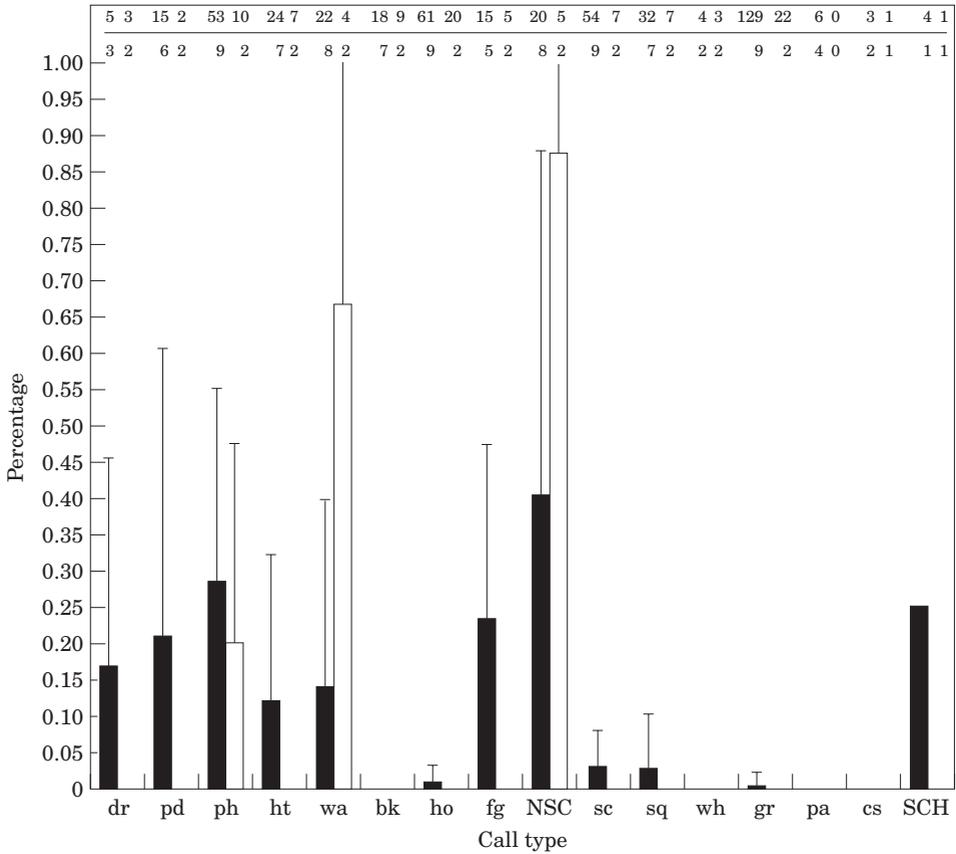


Figure 4. The percentage of calls that an individual heard to which the individual “responded”, averaged across individuals (lines show standard deviations; standard deviations not shown are as follows: subadult male wa, 0.47; subadult male NSC, 0.18). (■) adult males; (□) subadult males. The numbers above the bars represent the total number of calls heard by individuals in that age class (above), and the number of individuals who heard that call type during focal observations (below). See legend to Figure 1 for abbreviations, except for the following: pd, combined pant hoot and buttress drum; NSC, chorus of nonsubmissive calls; cs, female copulation scream; SCH, chorus of submissive calls.

monkeys, *Callicebus moloch* (Robinson, 1979); pygmy marmosets, *Cebuella pygmaea* (Snowdon & Cleveland, 1984); tamarins, *Saguinus oedipus* (McConnell & Snowdon, 1986)]. In some species distinctive loud calls are given by males as territorial displays, and these can elicit similar calls from one or more neighbors, sometimes producing chains of vocalizations across forest habitats [e.g., mangabeys, *Cercocebus albigena* (Waser, 1977); baboons, *Papio anubis* and *P. cynocephalus* (Waser, 1982); black and white colobus, *Colobus guereza* (Marler, 1972);

orang-utans, *Pongo pygmaeus* (Mitani, 1985b); blue monkeys, *Cercopithecus mitis* (Marler, 1973)]. Group members in many species exchange acoustically similar contact calls [e.g., macaques, *Macaca fuscata* (Green, 1975; Sugiura & Masataka, 1995); capuchins, *Cebus nigrivittatus* (Robinson, 1982); squirrel monkeys, *Saimiri sciureus* (Biben *et al.*, 1986; Boinski & Mitchell, 1992); baboons, *Papio cynocephalus ursinus* (Cheney *et al.*, 1996); gorillas, *Gorilla gorilla beringei* (Harcourt *et al.*, 1986)] or give similar calls simultaneously in “choruses”

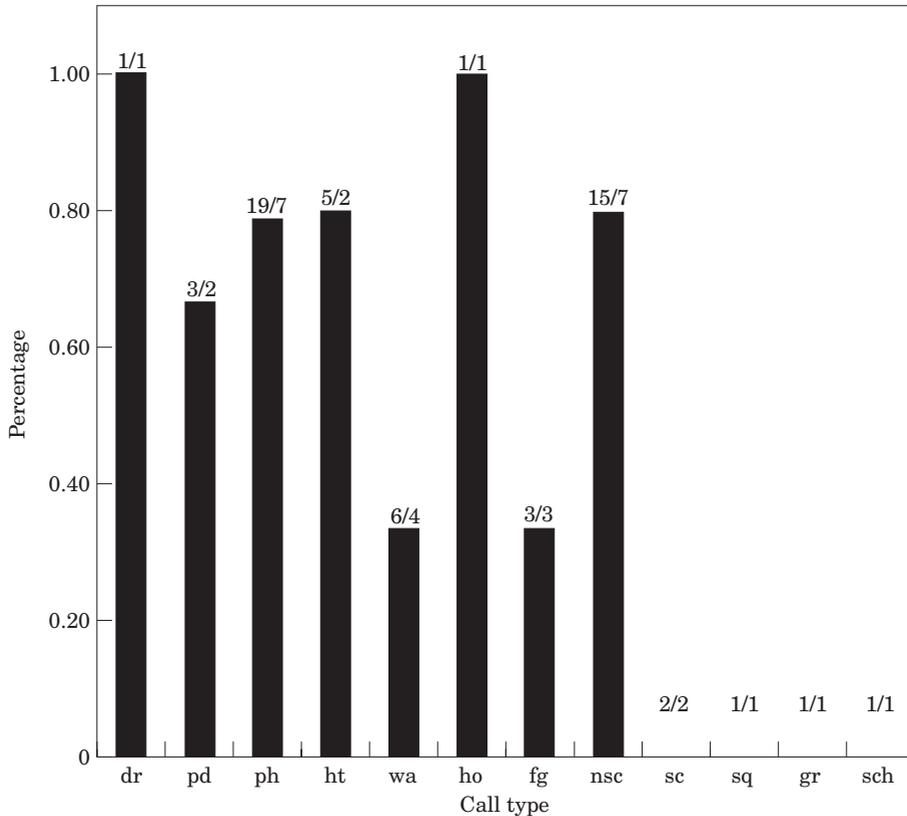


Figure 5. The percentage of “response” calls that were of the same type as the call heard, pooled across all individuals. Numbers above bars represent the total number of calls heard of that type (above), and the number of individuals who heard the calls (below). See legends to Figures 1 and 4 for abbreviations. The data are pooled because of the low number of calls heard by each individual for most call types.

[e.g., howler monkeys, *Alouatta seniculus* (Sekulic, 1982); chimpanzees, *Pan troglodytes* (Goodall, 1986)]. In contrast, normal human conversation typically involves the alternation of utterances that are dramatically different acoustically, although some repetition may occur (Tannen, 1987).

The results of this study indicate that chimpanzees, like other nonhuman primates, tend to interact vocally using acoustically similar calls. Calling rates were higher when other calls were audible, and temporally clumped calling within and between subgroups typically involved either chorusing or countercalling with calls of the same type as those just heard. Thus, there was no

evidence in this study that chimpanzee vocal exchanges exhibited uniquely human-like conversational qualities, such as an ordered exchange of different categories of acoustic signals.

In addition, the percentage of calls given that followed another vocalization (46%, range=0–84%) was similar to percentages reported for other species. For example, Kudo (1987) found that for seven types of calls given by wild mandrills (*Mandrillus sphinx*), from 3 to 41% of the vocalizations produced in each call type occurred within 5 s of hearing another call; in two groups of mountain gorillas (*Gorilla gorilla beringei*), 63 and 65% of close calls were given within

1 sec of hearing another close call (Harcourt *et al.*, 1986); and in baboons (*Papio cynocephalus ursinus*), 74% of female barks occurred within 5 min of hearing another female's bark, although only 19% of females in a series of 36 playback trials responded to contact barks within 5 min (Cheney *et al.*, 1996; see below for discussion of discerning true responses). Thus, in contrast to the qualitative impression that chimpanzees vocalize frequently and in unusually complex ways (e.g., Boehm, 1992), focal animal sampling revealed that individuals vocalized relatively infrequently, and that most calls were uttered spontaneously, as in other primate species.

Although chimpanzees produce temporally clumped vocalizations that sound alike to human listeners, it is possible that the animals perceive differences between the calls, and that their "exchanges" are therefore more complex than they seem. Acoustic analysis has revealed that some primate calls that sound the same to human observers are in fact distinct vocalizations that are used in different contexts and elicit different behavioral responses [e.g., coos in Japanese macaques, *Macaca fuscata*: Green (1975); grunts in vervets, *Cercopithecus aethiops*: Cheney & Seyfarth (1982); and screams in rhesus macaques, *M. mulatta*: Gouzoules *et al.* (1984)]. In some species, similar but distinct calls are exchanged in an orderly and predictable fashion, prompting the interpretation that vocal interactions in these animals exhibit conversational attributes [e.g., pygmy marmosets, *Cebuella pygmaea*: Snowdon & Cleveland (1984); squirrel monkeys, *Saimiri sciureus*: Biben *et al.* (1986)]. Given the cognitive and social complexity of chimpanzees, it would not be surprising if similar subtleties were discovered in their calls. If they are, chimpanzees could then be added to the list of nonhuman primates whose vocal interactions display rudimentary features of conversational exchange. Nevertheless, the results of this

study do not suggest that chimpanzee vocal "exchanges" are any more complex than those of other primates.

In a comprehensive review of African ape vocal behavior, Mitani (1996) concluded that there is no evidence that chimpanzee vocal behavior is qualitatively different from that of other primates. Boehm (1992) and Ujhelyi (1998), by contrast, have proposed that chimpanzee vocal behavior is more sophisticated than the vocal behavior of other primates, and therefore offers special insights into the evolution of language. The results reported here do not support this view. Although it remains possible that chimpanzees are communicating in unusually complex ways compared with other primates, substantially more quantitative data are needed before such a conclusion can be drawn.

Given that chimpanzees appear to have greater cognitive powers than other primates, including the ability to learn symbols during interactions with humans (Byrne, 1995; but see Tomasello & Call, 1997, for a more cautious interpretation in recognition of the fact that some chimpanzees used as experimental subjects have been reared in especially rich social environments), why is this comparative sophistication not reflected in their vocal behavior? One explanation is that, like the vocalizations of other primates, chimpanzee vocalizations are not symbolic in the way that words are (Noble & Davidson, 1996; Deacon, 1997). Even those primate calls that are thought to "refer" to features of the external environment (e.g., vervet alarm calls: Seyfarth *et al.*, 1980) differ markedly from words: their "meaning" appears limited to the connection between referent and sound, is relatively difficult to specify [e.g., an alarm call could refer to the predator or to the escape strategy (Owren & Rendall, 2000)], and could result from simple conditioning (Owren & Rendall, 1997). By contrast, human symbols (words)

are constructed from hierarchical webs of relationships that may involve external referents, but also depend on conventionalized interrelationships with other symbols (see Noble & Davidson, 1996; Deacon, 1997), and are generally acquired through association with other symbols, rather than by direct reference to external phenomena (Pinker, 1994).

Language is organized around the use of symbols, and the acoustic complexity of speech reflects the symbolic richness of human communication (Kohler, 1998; Lindblom, 1998; Studdert-Kennedy, 1998). If chimpanzees were communicating symbolically (*sensu* Deacon, 1997), we might expect their vocal “exchanges” to exhibit language-like organization. However, there is as yet no persuasive evidence that chimpanzees communicate symbolically in the wild. In a previous study (Clark & Wrangham, 1993), I attempted to determine whether a specific pant hoot variant referred specifically to the presence or character of food resources. Although the so-called “food pant hoot” was frequently given at fruiting trees, it was also given in other contexts, and I could not assign unambiguous semantic content to it. Similarly, Hauser & Wrangham (1987) and Hauser *et al.* (1993) tested experimentally the hypothesis that the use of food grunts by captive chimpanzees referred to the quantity and quality of food they were given. In this case, individual calling rates increased with increasing amounts of food, making it impossible to reject the possibility that calling rate simply reflected the affective state of the vocalizers (Mitani, 1996).

Some observers have suggested that wild chimpanzees use nonvocal signals symbolically, but, as with vocal signals, the evidence is inconclusive. Boesch (1991), working at the Taï Forest study site in Ivory Coast, found that when the alpha male produced successive buttress drumming bouts in the same place individuals joined him and rest

periods followed, but when this male drummed on buttresses along a direction of travel, individuals changed their travel direction to meet and travel with him. Boesch then suggested that the drumming performances symbolically encoded messages about rest and travel. However, there is no way to eliminate the possibility that listeners simply deduced the drummer’s current or future position, joined him, and then matched his behavior. Similarly, Savage-Rumbaugh *et al.* (1996) suggested that bonobos at the Wamba study site in the Democratic Republic of the Congo indicated travel direction by leaving visual signals in the form of flattened or broken vegetation along trails. In this case, there was no obvious way to assess whether the presumed signals were left intentionally, or were the byproducts of normal locomotor and social behaviors.

Although wild chimpanzee communication does not appear to be symbolic, the fact that captive chimpanzees can acquire some linguistic skills if they are reared with humans from infancy suggests that they have a limited capacity for symbol use, a potential that could have a specific neuroanatomical foundation (e.g., Gannon *et al.*, 1998). This raises two related questions: why isn’t their communicative behavior in the wild more complex, and, assuming that early hominids had cognitive powers at least equal to those of modern chimpanzees, what social and/or environmental change in hominid evolution stimulated the evolution of language?

Recent theorists have emphasized the need to explore cognitive and social, rather than vocal, continuities and discontinuities with nonhuman primates to understand the origin and evolution of language (e.g., Cheney & Seyfarth, 1990; Burling, 1993; Deacon, 1992; Ulbaek, 1992, 1998; Seyfarth & Cheney, 1997; Dunbar, 1996, 1998; Goody, 1997; Knight, 1998; Worden, 1998). For example, although chimpanzees may have the cognitive capacity for symbol use, they might not live

in social environments sufficiently cooperative to engender the web of indexical relationships that form the basis of symbols (Ulbaek, 1992, 1998; Savage-Rumbaugh & Rumbaugh, 1993; Deacon, 1997; Knight, 1998). Alternatively, the development of a Theory of Mind might be a necessary precondition for increased social and communicative complexity (Cheney & Seyfarth, 1990; Seyfarth and Cheney, 1997), or, reversing the causal relationship, the development of syntax might be necessary in order to represent other minds (Goody, 1997). In any case, the present study supports the view that the specific structures of chimpanzee calling bouts are of no special use for understanding the evolution of linguistic structures. If unique preadaptations for language are present in chimpanzees, they will probably be found in the behaviors and structures associated with vocal learning and flexibility, and in the organization of chimpanzee social interactions in general.

#### *Important biases and future directions*

Two important shortcomings in this analysis will need to be addressed in future studies to strengthen the results and help resolve the theoretical issues related to conversational exchange in chimpanzees. First, it was not possible to be certain in this study whether the calls given were in fact “responses” to other calls. Analyses of contact calling in Japanese macaques (Sugiura, 1993) and baboons (Cheney *et al.*, 1996) have shown that contact calls may clump because individuals are simultaneously responding to external stimuli, or because individuals repeat themselves without regard to other callers. Second, although most chimpanzee “responses” are of the same call type as calls just heard, many are not. Thus, a more fine-grained picture of variation in call “responses”, by call type, may yet reveal call exchange complexity in this species, a possibility that could bear directly on our understanding of the evolution of linguistic

structures. To surmount these two sources of bias, the inherent difficulties associated with collecting data on animals that do not remain in stable social groupings will need to be overcome. Methods for monitoring the vocal behavior of more than one individual in a subgroup at a time, and for monitoring more than one subgroup simultaneously, will need to be developed.

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