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Semiotic combinations in *Pan:* A comparison of communication in a chimpanzee and two bonobos

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Abstract

Communicative combinations of two bonobos *(Pan paniscus)* and a chimpanzee *(Pan troglodytes)* are compared. All three apes utilized ordering strategies for combining symbols (lexigrams) or a lexigram with a gesture to express semantic relations such as agent of action or object of action. Combinatorial strategies used by all three apes revealed commonalities with child language, spoken and signed, at the two-year-old level. However, many differences were also observed: e.g., combinations made up a much smaller proportion and single symbols a much larger proportion of ape production compared with child production at a similar age; and ape combinations rarely exceeded three semiotic elements. The commonalties and differences among three sibling species highlight candidate combinatorial capacities that may underlie the evolution of human language.

Keywords

animal language, bonobo, chimpanzee, evolution of communication, language acquisition, symbolic combination

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The evolutionary history of symbolic capacities is of great developmental interest. Developmental theorists Piaget (1962) and Werner (1948) emphasized the intertwining of phylogeny and ontogeny in symbolic development; others noted that the evolution of a species can be seen as a sequence of ontogenies that are modified over evolutionary time (Parker, Langer, & McKinney, 2000). Indeed, as stated by Parker and Gibson (1979), language could not evolve in any other sequence than that in which it develops.

While apes have not evolved humanlike language since diverging from the hominid line 5 million years ago (Stauffer, Walker, Ryder, Lyons-Weiler, & Hedges, 2001), any potential for symbolic communication in *Pan* is likely to have existed in the common ancestor. This argument is a product of cladistic analysis. Cladistics suggest that when all member species diverging from an evolutionary node (like that which gave rise to humans, bonobos, and chimpanzees) show the same capacities, the most parsimonious explanation is that those capacities existed in their common ancestor, even if those capacities were unexpressed (Byrne, 1995). These prehistoric phylogenetic stages of language, prerequisite to the more complex forms of *Homo sapiens*, could resemble early ontogenetic stages, similarly prerequisite to the complex structures of adult human language. A proponent of this idea, Bickerton (1990) has proposed the existence of 'protolanguage,' composed of telegraphic utterances having no syntactic marking and produced by language-competent chimpanzees and two-year-old children. One approach, therefore, to investigating the development and evolution of symbolic capacities is to investigate the existence of these capacities in our closest living relatives – chimpanzees (*Pan troglodytes)* and bonobos (*Pan paniscus)* – who, along with humans, comprise an evolutionary clade.

One theme pursued in the present article is that bonobos and chimpanzees have developed symbolic capacities roughly equivalent to those of a two-year-old child. Following Piaget, we also assert that the capacity level of the individual applies to various symbolic domains. It is therefore relevant to cross-species comparison in the language domain that we have established commonalities across the clade in the development of symbolic play (Lyn, Greenfield, & Savage-Rumbaugh, 2006).

In accord with the observations of Piaget (1962), McCune-Nicolich (1977), and Leslie (1987), bonobos and chimpanzees both manifest sequences of symbolic play that were similar to children's during the first years of life. There was also strong evidence that scaffolding of symbolic play by human caregivers promoted this competence, as it does in human children (Bondioli, 2001; Farver, 1993; Mannle, Barton, & Tomasello, 1992; Zukow, 1986). Some of the apes had achieved competence in a humanly devised symbol system – the visual lexigram system – while others had not. All of the apes went through the same basic sequence of symbolic-play development; however, only the apes with competence in the lexigram system, both bonobos and chimpanzees, were able to achieve what Leslie called 'true pretense.'

These commonalities among three species in early symbolic development in the domain of pretense are mirrored in the domain of communication. Greenfield and Savage-Rumbaugh (1991, 1993) explored pragmatic development in apes and found that both chimpanzees and bonobos, all competent in the lexigram system, used repetition to express pragmatic functions that were very similar to those expressed by two-year-old children: for example, confirmation and choosing between two alternatives (Ochs Keenan, 1977).

Further, gesture is a large part of the semiotic repertoire of apes in both ape–human communication (e.g., Bonvillian & Patterson, 1993; Greenfield & Savage-Rumbaugh, 1990) and ape–ape communication (Pika, 2008). Indeed, many accounts have placed gesture at the forefront of language origins (e.g., Bonvillian, Garber, & Dell, 1997; Corballis, 2002; Greenfield, Lyn, & Savage-Rumbaugh, 2008; Pika, 2008). Gesture is also the most flexible communicative mode for every ape species studied (e.g., Pika, Liebal, & Tomasello, 2003, 2005; Pollick & de Waal, 2007). Based on data from across the clade, we have recently concluded that, between one and two years of age, deictic gestures combined with representational symbols function similarly in the early development of symbolic combination for bonobos and chimpanzees (Greenfield et al., 2008), as they do for human children (Butcher & Goldin-Meadow, 2000; Goldin-Meadow, 2003; Greenfield et al., 2008; Iverson, Capirci, Volterra, & Goldin-Meadow, 2008; Ozcaliskan & Goldin-Meadow, 2005; Volterra, Caselli, Capirci, & Pizzuto, 2005). Further exploration of gestural communication by symbol-using apes in the present study may help shed more light on the role of gesture in language development and evolution.

In a pioneering study of English speech comprehension, Savage-Rumbaugh and colleagues (1993) carried out a direct comparison of the bonobo Kanzi and a two-year-old human child. In line with our hypothesis of a common level of development across various symbolic domains, Kanzi and the two-year-old child showed very similar levels of comprehension of English speech: both were able to comprehend and carry out English commands that involved one or two objects and an action. As one would expect from our comparative study of symbolic play, both two-year-old child and bonobo had the comprehension one would expect from a child at the end of the sensorimotor period.

Producing semiotic combinations: Background and the present study

Important similarities and differences have been reported between a language-competent bonobo *(Pan paniscus)*, Kanzi, and human children in the development of their early semiotic (meaningful) two-element combinations (Greenfield & Savage-Rumbaugh, 1990, 1991). Subsequently, a bonobo (Panbanisha) and a chimpanzee (Panpanzee) were co-reared in a symbol-rich environment allowing the opportunity to compare their communicative style and strategies with each other and with those of Kanzi, who had learned to communicate under somewhat different conditions. In this report we investigate whether the pattern of similarities and differences to human speech and language seen in Kanzi's data extends to another bonobo and to the other member of the clade, that is, to a chimpanzee, the third sibling species of *Pan* and *Homo*.

Semiotic combination in a bonobo

Greenfield and Savage-Rumbaugh (1990, 1991) investigated Kanzi's use of protogrammatical strategies. Symbol order was the most likely avenue for such strategies because the caregivers were all English speakers and therefore utilized the word-ordering strategies inherent in that language. The investigators used five basic criteria from classic child and chimp language studies to assess the presence of ordering strategies (as opposed to item-based constructions [Tomasello, 2003]):

(1) Each component of a combination must have independent symbolic status (Brown, 1973). (2) The relationship between the symbols must be reliable and meaningful (semantic) (Terrace, Petitto, Sanders, & Bever, 1979). (3) A strategy must specify relations between categories of symbols across combinations, not merely a relation between individual symbols (Bronowski & Bellugi, 1970; Terrace et al., 1979). (4) Some formal device, such as statistically reliable order (Braine, 1976; Goldin-Meadow & Mylander, 1984) must be used to relate symbol categories across combinations. (5) The strategy must be productive (Hill, 1978; Savage-Rumbaugh, Sevcik, Rumbaugh, & Rupert, 1985; Terrace et al., 1979; Terrace, Petitto, Sanders, & Bever, 1980). (5a) A wide variety of spontaneous combinations must be generated (Petitto & Seidenberg, 1979; Terrace et al., 1979, 1980). (5b) Utterances are not imitated (Petitto & Seidenberg, 1979). (5c) Some new strategies never modeled are created (required for strategy invention, but not strategy use).

Kanzi's symbolic productions satisfied these criteria. Analyzing his two- and three-symbol combinations, Greenfield and Savage-Rumbaugh (1990, 1991) found that Kanzi used his established vocabulary (criterion 1) to create meaningful combinations (criterion 2), that he ordered his combinations according to category (criterion 3), and that these orders were statistically reliable (criterion 4). Kanzi generated a wide variety of spontaneous combinations (criterion 5a), given that imitated combinations had been eliminated from the corpus (criterion 5b). Greenfield and Savage-Rumbaugh (1991) presented evidence that, in one case, Kanzi had created his own ordering strategy (criterion 5c) and 'taught' that strategy to his caregivers. Indeed, the strongest ordering strategy recorded was his own invention: 'lexigram precedes gesture.'

Prior comparison of the communication of Panbanisha (bonobo) and Panpanzee (chimpanzee)

Brakke and Savage Rumbaugh (1995, 1996) found that both Panbanisha and Panpanzee had the ability to acquire individual lexical symbols (without shaping or reward-based training) and this acquisition occurred in a similar manner. Similarities were also reported in the production, pragmatic force and comprehension of single symbols, as well as the comprehension of symbolic combinations (Brakke & Savage-Rumbaugh, 1995, 1996).

Research questions

- *Could another bonobo replicate Kanzi's achievements in the domain of protogrammar?* This question is relevant to the species generality of Kanzi's capabilities in symbolic combination. While the existence of similar capacities in another bonobo will not speak to the presence of such abilities in all bonobos, should another bonobo share Kanzi's abilities, we can infer that his achievements are not singular.
- *Could a chimpanzee replicate Kanzi's protogrammatical achievements*? This question is relevant to the generality of these achievements, shared by human children. Are these achievements also possible for the third species of the clade,

the chimpanzee? It is the key question that relates to the evolutionary baseline for the development of human grammatical capacities in the last 5 million years. If the answer to this question is affirmative, then the potential to combine symbols is present throughout the clade. This common potential would make these abilities a likely candidate as an ancestral foundation from which human grammar could have evolved following the evolutionary divergence of human beings from *Pan* about 5 million years ago.

- *What are the similarities and differences between the combinatorial symbolic capacities of* Pan *(bonobos and chimpanzees) and the third member of the clade, Homo sapiens? To the extent that similarities are found, where do they fall on the ontogenetic scale of human language acquisition?*

Methods

Participants and their environment

Our participants were Kanzi, a bonobo, Panbanisha, his half sister born five years later, and Panpanzee, a chimpanzee born within six weeks of Panbanisha. All three were reared at the Language Research Center, Atlanta, Georgia in a within- and cross-species communicative environment. Travel in the woods and climbing trees, important activities in the wild, were part of all three apes' environment.

Their communicative environment consisted of gesture, speech, and written visual symbols (lexigrams) placed on a keyboard. The lexigram keyboard was made available to the apes at all times and some of the available keyboards emitted the sounds of a computer-synthesized English word when the corresponding key was touched. While utilizing any of these keyboards, the caregivers were instructed also to communicate in English. Therefore, English and lexigram use were paired in the communicative environment of the apes and caregivers naturally used English word-order rules when utilizing the keyboards.

Emphasis on keyboard use and spoken English was begun earlier with Panbanisha and Panpanzee than with Kanzi (before they were six weeks old, as opposed to Kanzi's several months old). Unlike Kanzi, who was initially exposed to a keyboard of six symbols during reward-based training sessions with his mother (the first keyboard that he used himself contained 12 symbols), Panbanisha and Panpanzee were initially exposed to a keyboard of more than 256 symbols and were expected to learn the use of these symbols without specific training.

Almost from birth, Panbanisha and Panpanzee were generally in the company of at least one human caregiver and each other 24 hours a day, seven days a week. During the last months of the study, they slept with older bonobos at night (Brakke & Savage-Rumbaugh, 1995). For the first two-and-a-half years of his life, Kanzi, in contrast, was in the care of his mother, who was being given language training. It was not until he was separated from his mother at age two-and-a-half that he began to display regular intentional symbol use (Savage-Rumbaugh, McDonald, Sevcik, Hopkins, & Rupert, 1986). The separation, which was for breeding purposes, lasted four months; when his mother returned, Kanzi chose to stay in the company of his human caregivers most of the time (Greenfield & Savage-Rumbaugh, 1990).

These different rearing histories were reflected in a difference in the timing of the first meaningful lexigram use. Whereas Kanzi produced his first meaningful lexigram at 30 months of age, Panbanisha and Panpanzee produced theirs around age one, a starting point very similar to that of a typically developing human child.

Vocabulary size. At the beginning of the period of the present analysis, Panbanisha had a productive vocabulary of about 105 lexigrams and Panpanzee had a productive vocabulary of about 70 lexigrams (Brakke & Savage-Rumbaugh, 1996). In children, the emergence of grammar is strongly dependent on vocabulary size, and most children make the passage into multiword speech with vocabularies of between 50 and 200 words (Bates & Goodman, 1997). Hence, we see that both apes had the vocabulary building blocks that would give them the potential to systematically combine their individual lexigrams. The independent symbolic status of most of the elements used in combinations had been established through formal vocabulary tests of comprehension and production. The bonobo, Panbanisha, had a larger vocabulary at the outset of the study period, began lexigram use slightly earlier than Panpanzee, and had somewhat more extensive speech comprehension skills (Brakke & Savage-Rumbaugh, 1995, 1996).

The independent symbolic status of 80% of the vocabulary that Kanzi used in his combinations had been established at 46 months of age, 20 months prior to the analysis of his combinations (Greenfield & Savage-Rumbaugh, 1990, 1991). At 46 months of age, Kanzi had a productive vocabulary of just under 50 lexigrams, and his vocabulary was still on an upward curve (Savage-Rumbaugh et al., 1986). Extrapolating this curve to 66 months of age, when our analysis began, we can estimate that he would have had a vocabulary of about 100 lexigrams, quite similar to the size of Panbanisha's vocabulary when we began the study of her combinations.

Data collection

During the study period of almost four years, virtually all uses of the keyboard by Panbanisha and Panpanzee, as well as communicative gestures used in combination with lexigrams, were recorded by hand by the caregivers and input into a computer database at the end of the day; this would have provided more than eight hours of data collection per day. This procedure provided the researchers with an exhaustive written record of their symbol use. The database contained the utterance (which could include lexigram(s), gesture(s), or a combination of lexigram with gesture), date, record number, ape, researcher, codes as to pragmatic force of the utterance, behavioral concordance notes, and a short contextual note. Behavioral concordance – the relationship between the utterance and the ape's behavior, particularly his or her behavior subsequent to the utterance – was the main clue as to semantic relations and pragmatic force. Examples of utterances and their behavioral concordance and pragmatic force are reported in the context column of Table 1 (pragmatic force results for Panbanisha and Panpanzee's complete corpus are reported in Brakke & Savage-Rumbaugh, 1996). Requests and indicatives (statements, comments, spontaneous naming) were the two types of pragmatic force that appeared in our data.

The same general procedure was operative for Kanzi's data collection (for details, see Greenfield & Savage-Rumbaugh, 1990, 1991), with one important difference. Kanzi had at least one human caregiver with him recording his communicative productions nine hours a day, but contextual notes were provided only when there was a second caregiver present to function as an observer. This contextual description in the utterance database was our basis for coding combinations as to their semantic meaning. When the ape was with only one caregiver, the data would be excluded from our corpus for lack of contextual information. We estimate that two caregiver/researchers were present with Kanzi about four-and-a-half hours per day. For all three apes, the data collection procedures were similar to observational protocols used in classic studies of child language; these provided the comparative foundation for this study (Bowerman, 1973; Brown, 1973).

In accordance with the level and purpose of our data analysis, note that gestures were reported functionally. Deictic gestures are represented in our transcriptions through the use of /dg for deictic gesture. In addition, the apes used representational gestures, for example, the American Sign Language signs for 'more' and 'tickle,' and clapping their hands to denote 'chase .' These gestures and others are glossed as representative English words (e.g., 'more,' 'tickle,' and 'chase' respectively) and are labeled with an '/rg' for representational gesture in our transcriptions.

As a reliability check, real-time recording was checked against four-and-a-half hours of videotape. Thirty-seven out of 46 utterances, or 80%, were noted by both the real-time and the video observer (the other 11 were noted only by the video observer) and there was 100% agreement on the lexigram that had been used when both observers noted the utterance. Hence, we conclude that our corpus is highly reliable, but an underestimation of quantity.

Corpus

The data reported here for Panbanisha and Panpanzee are based on the complete corpus of two-element combinations (two lexigrams, one lexigram plus one gesture, or two gestures) for five months, up to the virtual end of the joint raising period. Two-element combinations comprised most of the apes' combinations, and so were numerous enough for statistical analysis. When the corpus began, Panpanzee, the chimpanzee, and Panbanisha, the bonobo, were three-and-a-half years old.

Kanzi's corpus for the study of combinations began when he was five-and-a-half years of age and, like the other two apes, covered a period of five months. Although he was two years older than Panbanisha and Panpanzee during the period of his data analysis, there was no indication that he reached a more advanced stage of two-word combinations.

Human input

Nine hours of videotape from Panbanisha and Panpanzee's study period were analyzed to assess human communicative input to them. Input to Kanzi had been analyzed in this same way (Greenfield & Savage-Rumbaugh, 1990, 1991). These data on input put us in a unique position to distinguish creative innovations from observational learning, both of which are important in human language acquisition.

Direct imitations of single or combined lexigrams produced by human caregivers, utterances without a clear situational context, as well as any utterances that were structured by the caregivers were eliminated. Imitations had to be immediate and included partial imitations (e.g., one lexigram repeated by the ape out of a complex lexigram sentence produced by the human caregiver). An example of caregiver structuring would be a request for conversational repair, e.g., 'Say that more clearly.' While we acknowledge and indeed have studied the role of repetition in conversational competence (Greenfield & Savage-Rumbaugh, 1993), the goal of eliminating partial or complete imitations and caregiver-structured utterances was to focus on the most creative aspects of symbolic combination, as we were interested in combinatorial productivity. Thus, we had very conservative criteria for the study of combinatorial creativity.

Unselected and complete corpora

Rivas (2005) notes the importance of utilizing unselected corpora. Our analyses are based on five months of unselected communications taking place and recorded over many hours a day. Moreover, we are unique in publishing our complete corpora. Kanzi's five-month corpus of spontaneous two-element combinations containing at least one lexigram was published by Greenfield and Savage-Rumbaugh (1991). Panbanisha and Panpanzee's five-month corpora of spontaneous two-element combinations (2 lexigrams, gesture + lexigram, 2 gestures) are presented as an online appendix.[1]

Coding and analysis of symbol combinations

The coding followed classical methodology for studying children in the two-word stage (Brown, 1973; Goldin-Meadow & Mylander, 1984; Schlesinger, 1971) and followed the coding scheme of Kanzi's utterances (Greenfield & Savage-Rumbaugh, 1990) as closely as was possible, given some innovative semantic relations created by Panbanisha and Panpanzee. For example, Panpanzee and Panbanisha frequently made affirmative–action combinations (YES + action lexigram) and this type of combination was never produced by Kanzi. (Coded semantic functions, definitions, examples, and contexts are presented in Table 1.)

The first author was the primary coder, trained in the coding scheme by the second author, who had coded Kanzi's data. An independent reliability coder (not an author) coded 140 randomly selected two-element combinations (70 for Panbanisha and 70 for Panpanzee, 11% of the corpus for each ape). The coders agreed on 253/280 individual elements (90.71%; $\kappa = .88$) and 118/140 two-element combinations (84.29%; $\kappa = .84$). Subsequently, the second author reviewed the entire corpus as presented in the online appendix[1]. Based on consulting the relevant context in the original record, minor adjustments in assigning combinations to categories of semantic relation were made by mutual agreement between the two authors.

Differences between the participants were tested by means of chi-square analyses. We also utilized binomial tests to see whether each ape utilized a consistent ordering strategy to express a particular semantic relation. For each semantic relation, the dominant order for combining two lexigrams and the dominant order for combining a lexigram and a gesture were tested separately against chance. Because of the symmetry of conjoined

Table 1. List of all utterance type codes, their definitions, examples from the data, and the context in which the example was produced

Name	Definition	Example	Context for example
Agent	someone or something which causes or instigates an action or process – has its own motivating force.	indicates agent/dg – in CHASE + indicates agent/dg	gesturing to the person she wants to chase with; they then chase (request)
Action	a physical act, as indicated by the context (see Greenfield & Lyn, 2006 for details on operationalizing intentional action)	TICKLE – in TICKLE + indicates agent/dg	asking to play tickle with someone (request) where the individuals tickle after the request
Object	someone or something that is either suffering a change of state or receiving the force of an action.	BALL – in SLAP BALL	Panbanisha asking to play slapping with the ball (request) where the act subsequently takes place
		indicates object/dg – in OPEN + indicates object/dg	pointing to a door, wanting to open it (request)
Entity	any thing or person with a separate existence, in a semantic relation with another communicative element, but not an agent, object, or goal of action	MILK – in MILK + indicates milk/dg	pointing to the milk while drinking the milk (indicative)
Demonstrative	deictic indication of location or entity	indicates milk/dg – in MILK + indicates milk/dg	gesturally indicating the milk, asking for milk (request)
Attribute	an attribute which could not be known from the class description	more/rg – in more/rg WATER	asking for more water play, which then continued (request)
Goal	an action's goal object or location/dg	indicates location/dg – in GO + indicates location/dg	Panpanzee gesturally indicating a location where she wants to go, then going there (request)
		MATATA – in OPEN MATATA	Panbanisha wants to open the door to visit Matata; they then go in (request)

(Continued)

Table 1. *(Continued)*

Name	Definition	Example	Context for example
Location	a place associated with an entity	HILLTOP – in HILLTOP SURPRISE	Panpanzee wants to go to hilltop to get a surprise; they then go (request)
Recipient	an animate entity with its own motivation that is receiving an object	MATATA – in SURPRISE MATATA	Panbanisha sees Linda bringing a surprise to Matata (indicative)
Affirmative	use of the lexigram 'YES' for affirmation	YES – in YES PLAY	asking to play, which they then do (request)
Negative	denial or nonexistence	NO – in NO CHASE	Panbanisha tries to get Kanzi to play unsuccessfully, then tells her caregiver that Kanzi does not want to chase
Comitative	indicating an animate being in whose company something is done	indicates animate being/dg – in TRAILER + animate being/dg	Panbanisha was going to the trailer and pointed to Panpanzee to see if she would come along; they then went to the trailer (request)
Instrument	a tool for doing something	KEY – in OPEN KEY	Panbanisha wants Karen to open the door with the key, which she does (request)
Possession	an inanimate entity associated with a person	no clearcut example found	
Possessor	a person associated with an inanimate entity	no clearcut example found	
Performative	symbol that is an act in itself; it cannot be true or false	QUESTION – in QUESTION REFRIGERATOR	Panbanisha asking if she can go to the refrigerator (request)

Note: For every semantic function, it was possible to express that function with the pragmatic force of request/imperative or indicative (shown in parentheses in the Context column). Pragmatic force was not taken into consideration when selecting examples for the various semantic functions. Semantic functions could be expressed by either lexigram or gesture. Categories are based on Greenfield and Smith (1976).

Key: /dg = deictic gesture. /rg = representational gesture. Words all in capital letters indicate a lexigram. If an example was constructed by only one ape, the name is attached. If it is general to both apes, no name is given.

relations (e.g., conjoined actions), only the dominant order for combining a lexigram and a gesture could be tested. Because there are two possible orders of two elements, the chance probability was considered to be .5 for each binomial test.

Results

Overview of the data and comparison with human children

Combinations of two or more elements accounted for 16.1% of Panbanisha's utterances (1043/6492) and 15.6% of Panpanzee's utterances (978/6250), respectively. Both apes produced a significantly higher proportion of combinations (vs. single symbols) than Kanzi (10.4% or 1422/13,673 were combinations), (χ^2 for Panbanisha vs. Kanzi (1, N = 20,165) = 122.99, $p < .001$; χ^2 for Panpanzee vs. Kanzi (1, N = 19,923) = 96.9, $p < .001$), but were not significantly different from each other (χ^2(1, N = 12,742) = 0.42, $p > .05$). This pattern would seem to be a result of earlier and more intense experience both with the lexigram system and with cross-species communication with humans on the part of Panbanisha (bonobo) and Panpanzee (chimpanzee) than Kanzi (bonobo) had.

While Panbanisha and Panpanzee's pattern had moved slightly in the direction of human children, in comparison with Kanzi, their proportion of combinations was still much lower than that of human children and closer to that of Kanzi. By age two, one child in Greenfield and Smith's (1976) study of the one-word stage and the transition to combinatorial language had a corpus in which 73% of the utterances combined more than one morpheme; by 22 months of age, the other child in the study had a corpus in which 55% of the utterances combined more than one morpheme.

There was an upper limit on complexity for the apes that is not found for human children. Whereas Panbanisha began using single lexigrams meaningfully at roughly the same age (11 months) as children raised in a North American cultural environment and Panpanzee was not too far behind (20 months), complexity did not progress in the same manner. For example, the three children in Brown's sample had, by age three-and-a-half, all reached a mean length of utterance of four morphemes, with maximum length somewhere around 13 morphemes (Brown, 1973). At the same age, Panbanisha and Panpanzee's mean length of utterance was under two semiotic elements (lexigrams, gestures); anything over three elements was a rarity in the corpus, with corresponding limitations on complexity.

After the elimination of immediate imitations and productions without contextual information, our final corpus of spontaneous two-element combinations consisted of 642 two-element combinations for Panbanisha, 637 for Panpanzee, and 731 for Kanzi. In terms of pragmatic force, the two-element corpora were made up mostly of requests (516/642 utterances – 80% – were requests for Panbanisha and 590/637 utterances – 93% – requests for Panpanzee), with the remainder constituting various forms of indicative (Lyn, Greenfield, Savage-Rumbaugh, Gillespie-Lynch, & Hopkins, 2010). These unselected corpora are much larger corpora than are found in the classic child language studies.

Kanzi produced a significantly higher proportion of requests than either Panpanzee or Panbanisha with 96% (702/731) of his two-element combinations being requests

(Panpanzee: $\chi^2(1, N = 1368) = 7.55, p < .01$; Panbanisha: $\chi^2(1, N = 1373) > 23, p < .001$). Panpanzee also produced a significantly higher proportion of requests than Panbanisha ($\chi^2(1, N = 1279) > 23, p < .001$). Although there were individual differences in the proportion of the three corpora that were requests, all three apes had a higher percentage of requests than children. For example, in a controlled comparison, Greenfield and Smith (1976) found that two boys studied from their first words to about two years of age used their lexicon to indicate objects much more often than they used their lexicon to request objects. One boy indicated objects 80.5% of the time, while requesting them in only 19.5% of the cases. The other boy indicated objects 56.7% of the time, while requesting objects in the remaining 43.3% of cases.

Semantic relations

The parsing of action events into representational categories such as action, agent, object, and location is universal in child language, according to Brown's (1973) cross-linguistic analysis. In samples of children acquiring English, Finnish, Swedish, Samoan, and Spanish, the percentage of two-word utterances falling into the eight most common semantic relations range across the different samples from 30% to 81% (Brown, 1973). These relations are: Agent–Action; Action–Object; Agent–Object; Action–Location (Goal), Entity–Location, Possessor–Possession, Entity–Attribute, Demonstrative–Entity. Seven of Brown's eight most prevalent semantic relations are represented in our corpora and, in fact, make up a majority of expressed relations (Panpanzee, the chimpanzee, 362/637 [57%], Panbanisha 367/642 [57%], and Kanzi 554/731 [76%]). Thus, both the two bonobos and the chimpanzee fall within the quantitative range of human children around the world for their relative emphasis on expressing Brown's most prevalent semantic relations.

As with the children in Brown's study, the remaining two-element combinations in the ape corpora were equally structured. Often, they were constructions that involved at least one low-frequency semantic function. Examples are Location–Instrument or Instrument–Object. Sometimes, they were simply low-frequency combinations of two semantic functions each of which individually appeared in the top eight. An example of one of those is Attribute (of) Action, where both Attribute and Action are common semantic functions, but the combination is infrequent. Some of the combinations that did not fit into Brown's top eight were quite frequently constructed by the apes. An example of this type of relation is Conjoined Action (e.g., CHASE BITE, a play sequence). One semantic relation that is frequent for children in many cultures was never constructed by the apes: Possessor-Possessed. As the online appendix[1] shows, this type of combination was not present in either Panbanisha's or Panpanzee's data. Table 2 presents the most frequent types of two-element combinations produced by each ape.

Panbanisha and Panpanzee also co-constructed three new meaning relations involving affirmatives (YES used to ask permission for something); one was Affirmative–Goal (YES OUTDOORS, to ask to go outdoors) used only once by Kanzi; the second was Affirmative–Entity (YES BANANA, to ask for a banana), again used only once by Kanzi; the third was Affirmative–Action (YES HUG, to ask for a hug), never used by Kanzi. These permission-asking constructions were quite frequent.

Ordering strategies for expressing different semantic relations

Panpanzee and Panbanisha innovated a systematic ordering strategy to express these semantic relations involving affirmation (affirmative first; goal, entity, or action second) (see Table 2). As Table 2 shows, these semantic ordering strategies were statistically significant for both apes for Affirmative–Action and Affirmative–Goal for both apes and for Affirmative–Entity for Panbanisha. While their human caregivers, on occasion, used two of these constructions – Affirmative–Entity (7 times) and Affirmative–Action (17 times) – they used them as responses to the apes' requests (e.g., YES we can GO outdoors). The creativity and originality of the 'YES' combinations lay with the apes.

Table 2 presents all of the semiotic ordering strategies utilized by the apes with specific meaning relations (e.g., Action–Object order vs. Object–Action order) for the two-element combinations in which at least five examples were found for at least one ape (a full list of all meaning relations found is presented in the online appendix.[1] Table 2 shows that Panbanisha, Panpanzee, and Kanzi utilize lexigrams and gestures to construct the same range of meaning relations and utilize many statistically reliable ordering strategies to construct their combinations. What this means concretely in the case of lexigram–gesture combinations is that, for example, ENTITY Demonstrative/g was significantly preferred to the opposite order, Demonstrative/g ENTITY, by all three apes; that is, the gesture-last order was significantly preferred by both species. (Here and throughout, we use capital letters to denote lexigrams.) In the case of Action–Goal, the gesture is placed last by Panpanzee no matter which semantic element is gesturally expressed (e.g., ACTION Goal/rg [or dg] as well as GOAL Action/rg). In the case of lexigram–lexigram combinations, however, our example shows that both Panbanisha and Panpanzee significantly preferred the order ACTION–GOAL to the order GOAL–ACTION.

Binomial tests show 27 examples of statistically significant ordering preferences in Table 2, some for lexigram–lexigram combinations, others for lexigram–gesture combinations; 27 are significant at the .05 level or better, 21 are significant at the .01 level or better, and 16 at the .001 level. Out of 46 possible tests represented in this table (excluding low frequency data that are not statistically testable), one would expect around 2 by chance at the .05 level and fewer than 1 at the .01 and .001 levels, suggesting that our results are not a product of random ordering in the construction of semantic relations, but reflect systematic combinatorial strategies. Looking only at lexigram–lexigram combinations, out of a possible 24 tests, one would expect fewer than 1 to be significant at the .05 level and our data show 9 (including 5 at .01 and 2 at .001 – both expected to be essentially zero).

In addition to identifying significant ordering strategies, it is also of interest to know whether gestures were more frequent in certain constructions. Deictic gestures were extremely popular; all three apes used gestures most frequently in the construction consisting of a deictic gesture plus a lexigram to name the indicated object or place.

Co-construction with whom?

Table 3 compares the number of preferential symbol orders that were shared between Panbanisha, Panpanzee, Kanzi, and the human caregivers. Surprisingly, the humans' input does not seem to be the main drive behind the apes' ordering preferences. By far the greatest number of common orders among any pair of respondents (9) occurs in the

Table 2. The most frequent types of two-element combination constructed by Panbanisha, Panpanzee, and Kanzi

	Panpanzee			Panbanisha			Kanzi		
	Lexigram only	Utterances with a gesture		Lexigram only	Utterances with a gesture		Lexigram only	Utterances with a gesture	
		Gesture first	Gesture last		Gesture first	Gesture last		Gesture first	Gesture last
Affirmative–Action	20*	0	4	42***	0	0	0	0	0
Action–Affirmative	7	0	0	13	0	0	0	0	0
Action–Agent	8	0	22^^^	1	0	40^^^	3	0	116^^^
Agent–Action	8	2	0	2	2	0	6	7	0 (2 G/G)
Attribute–Action	3	0	8^	5	0	0	2	0	0
Action–Attribute	1	0	0	1	0	0	4	0	0
Action–Goal	55***	1	14	37**	1	6	10	0	0
Goal–Action	14	3	32^^^	17	0	22^^^	16	0	30^^^
Action–Instrument	8*	0	2 (1 G/G)	4	0	0	2	0	0
Instrument–Action	2	0	5^^	0	0	0	2	0	0
Action–Object	10	1	8^^	9	0	32^^^	34**	0	5
Object–Action	6	0	3	7	1	0	13	2	0
Affirmative–Entity	8	0	2	15*	0	0	0	0	0
Entity–Affirmative	5	0	0	5	0	0	0	0	1
Affirmative–Goal	18**	0	1	32*	0	3	1	0	0
Goal–Affirmative	3	0	0	14	0	0	0	0	0
Agent–Object	0	0	0	0	0	0	0	1	0
Object–Agent	0	0	1	0	0	0	0	0	7^
Attribute–Entity	10	1	1	7	0	1	9	0	1
Entity–Attribute	4	0	0	6	0	1	11	1	0
Demonstrative–Entity	0	14	0	0	20	0	0	67	0
Entity–Demonstrative	0	0	87^^^	0	0	57^^^	0	0	182^^^
Entity–Location	8	0	38^^^	34	0	34^^^	12	0	0
Location–Entity	10	2	0	27	4	1	18	0	1
Goal–Instrument	7	1	2	2	0	2	2	0	0

Table 2. (Continued)

	Panpanzee			Panbanisha			Kanzi		
	Lexigram only	Utterances with a gesture		Lexigram only	Utterances with a gesture		Lexigram only	Utterances with a gesture	
		Gesture first	Gesture last		Gesture first	Gesture last		Gesture first	Gesture last
Instrument–Goal	8	0	2	1	0	0	0	0	0 (1 G/G)
Instrument–Object	0	0	6^ (1 G/G)	0	0	1	1	1	0
Object–Instrument	0	0	0	0	1	0	0	0	0
Conjoined Actions	77	0	15^^^	19	0	16^^^	85	2	5 (4 G/G)
Conjoined Entities	22	1	1	32	1	1	25	0	0
Conjoined Locations	4	0	1	22	0	1	7	0	0
Total	**326**	**26**	**257**	**354**	**30**	**218**	**263**	**81**	**355**

Note: The table consists of meaning relations in which at least five examples were found for at least one ape (the minimum required for statistical significance with binomial testing); a complete corpus of Panpanzee's and Panbanisha's two-element combinations (two lexigrams, lexigram + gesture, and two gestures) is presented in the online appendix.[1]). A corpus of Kanzi's two-element combinations (two lexigrams, lexigram + gesture) is found in the Appendix to Greenfield and Savage-Rumbaugh (1991). In addition, Kanzi's gesture-gesture combinations are included in this table. G/G = gesture–gesture combination.
Statistical analysis: Semiotic ordering for lexigram combinations: * $p < .05$, ** $p < .01$, *** $p < .001$. Semiotic ordering for lexigram-gesture combinations: ^ $p < .05$, ^^ $p < .01$, ^^^ $p < .001$. For each semantic relation, placement of gesture (gesture first or gesture last) has been collapsed across meaning orders in order to separate gesture placement preference from meaning order preference.

Table 3. Number of ordering strategies in the same direction and reaching statistical significance for both members of a pair

	Panbanisha	Panpanzee	Kanzi
Panpanzee	9		
Kanzi	3	3	
Humans	3	2	1

Note: Both gesture–lexigram and lexigram–lexigram ordering strategies were counted.

pair that were co-reared, Panbanisha and Panpanzee, even though they were not of the same species. That is, Panbanisha, a bonobo, shared more symbol-ordering conventions with her constant companion, Panpanzee, a chimpanzee, than she did with Kanzi, a conspecific (and her half-brother) and many more than any of the apes did with their human caregivers.

While English-speaking children have been shown in many studies to follow English word order quite reliably at the two-word stage (Brown, 1973), Kanzi did this for only one semantic relation, even though his only language model was provided by English-speaking caregivers. However, in languages where word-order models are more variable, human children may select one order or may simply reflect the variability that they hear around them. Panbanisha and Panpanzee have multiple models – from each other and from Kanzi, in addition to models provided by their human English-speaking caregivers. Nonetheless, they follow their human models more than they follow Kanzi; and they follow each other's semiotic orders most of all. They share three lexigram orders and six semantic relations where they produce the gesture last.

Just as simple human languages – such as pidgin or home sign – become more syntacticized across time when they are transmitted at a young age from generation to generation (Bickerton, 1990; Senghas, 2003), so there is an increase in the protosyntactic device of symbol order between the two generations of apes, where the second generation learned at a much younger age than the first. Whereas Kanzi used available word-order models less than human children do, Panpanzee and Panbanisha are in the human range for use of word-order models (Brown, 1973).

Lexigram–gesture combinations: Gesture last

Kanzi was shown to spontaneously create an ordering strategy of his own by overwhelmingly placing gesture last in his lexigram–gesture combinations (Greenfield & Savage-Rumbaugh, 1991). Like Kanzi, Panbanisha and Panpanzee also constructed 'gesture-last' combinations across a wide range of meaning relations. Panpanzee: gesture was last in 262 out of 293 combinations of lexigram and gesture, $p < .0001$, binomial test. Panbanisha: gesture was last in 229 out of 259 combinations of lexigram and gesture, $p < .0001$, binomial test. Humans place gesture first in 29 out of 33 combinations of lexigram and gesture, $p < .0001$, binomial test. Hence, Panpanzee and Panbanisha are strongly deviating from the human model in the placement of gesture in semiotic combinations. These figures for Panbanisha and Panpanzee are based on the total corpus (found in the online appendix[1]), not just the meaning relations in Table 2. Panbanisha and Panpanzee generalized the gesture-last strategy further than Kanzi: to Action-Object, Entity-Location, Conjoined Actions, and (Panpanzee only) Instrument-Object (Table 2).

Six out of nine total ordering strategies that Panbanisha and Panpanzee shared were lexigram–gesture combinations. Kanzi also shared two of his lexigram–gesture preferences with Panbanisha and Panpanzee – Entity before Demonstrative gesture, and Action before Agent gesture. In contrast, the human caregivers preferentially ordered only one lexigram–gesture combination – Agent (gesture) before Action (lexigram) (19 Agent–Action; 0 Action–Agent). This pattern of humans using the opposite order shows that gesture-last was an ape, not a human creation. In addition, human caregivers tended to use lexigrams rather than gestures – only 8 other lexigram–gesture combinations were recorded for the human caregivers.

Gesture–gesture combinations

Gesture-gesture combinations (likely undercounted for all apes because of lexigram focus during data collection) were recorded only for Kanzi and Panpanzee. For example,

> **Panpanzee**: Ape gestures toward caregiver's keys (**instrument**), then to the keyhole (**object**) in the door. Caregiver uses key to open door, and they leave room together. (Gesture–gesture combination, request)

In human children, gesture–gesture combinations are constructed by hearing children at the early stages of their language development (Guidetti & Nicoladis, 2008; Tomasello & Camaioni, 1997; Volterra & Iverson, 1995).

Differential ordering strategy

Depending on whether they are using gesture or not, Panbanisha and Panpanzee constructed a different ordering strategy within one meaning relation. When combining an action and a goal, Panbanisha and Panpanzee place the action first when utilizing only lexigrams (Table 2; lexigram–lexigram combinations: Panpanzee Action–Goal – 55, Goal–Action – 14, $p < .001$; Panbanisha Action–Goal – 37, Goal–Action – 17, $p < .01$, binomial tests), but place goal first when combining lexigram with gesture (lexigram–gesture combinations: Panpanzee Action–Goal – 15, Goal–Action – 35, $p < .01$; Panbanisha Action–Goal – 7, Goal–Action – 22, $p < .01$, binomial tests).

> **Panbanisha**: Ape touches the OPEN lexigram (**action**) and then touches the DOG lexigram (**goal**). Panbanisha is asking for her caregiver to open the door so they could visit the dogs**.** Panbanisha's caregiver has already said several times that they could not go to the dog pen to play with the dogs anymore. In this instance she asked someone else. (Lexigram–lexigram combination, request)

> **Panpanzee**: Ape touches the MATATA lexigram (**goal**) and then gestures to go (**action**), wanting to go see Matata (Panbanisha's mother). Her caregiver says they will see Matata later. (Lexigram–gesture combination, request).

Emphasis on living beings vs. tools: A difference between chimpanzee and bonobo

While Panbanisha's two-element combinations overwhelmingly refer to a social relation (combinations including an agent, a recipient, or a comitative, $n = 50$) rather than to a tool relationship (combinations including an instrument, $n = 12$), Panpanzee's two-element combinations are balanced between social relations ($n = 42$) and tool relations ($n = 47$). A chi-square test compared the ratio of social relations and tool relations in Panpanzee and Panbanisha; the *Pan troglodytes* (Panpanzee) expressed a significantly higher ratio of instrument relations ($\chi^2(1, 151) = 17.2, p < .001$). Kanzi's data are consistent with interpreting this as a species difference rather than an individual difference: in his entire corpus of 731 two-element combinations, Kanzi constructed only 9 tool relations, in comparison with 152 social relations (Greenfield & Savage-Rumbaugh, 1991). He too constructed significantly fewer tool relations than did Panpanzee ($\chi^2(1, 246) = 75.6, p < .001$). In this, the chimpanzee differed from human children, for whom the expression of instrumental relations is relatively infrequent (Brown, 1973), while the bonobos resembled human children in this respect.

Discussion

Could another bonobo replicate Kanzi's achievements in the domain of proto-grammar? Could a chimpanzee replicate Kanzi's protogrammatical achievements?

The answer to both of these research questions is yes. Both Panbanisha, a bonobo, and Panpanzee, a chimpanzee, utilized their established vocabulary (criterion 1) to create meaningful combinations (criterion 2), ordered their combinations according to category (criterion 3), and produced statistically reliable orders (criterion 4). Panbanisha and Panpanzee generated a wide variety of spontaneous combinations (criterion 5a), given that imitated combinations had been eliminated from the corpus (criterion 5b). Additionally, Panbanisha and Panpanzee created a novel ordering strategy, utilizing lexigrams – Affirmative before Goal – and all three apes placed gesture last across many semantically diverse situations, something that did not originate with their human caregivers.

What are the similarities and differences between the combinatorial symbolic capacities of Pan *(bonobos and chimpanzees) and the third member of the clade*, Homo sapiens*? To the extent that similarities are found, where do they fall on the ontogenetic scale of human language acquisition?*

We found similarities between the semantic relations in children's telegraphic language (in both spoken language and 'invented' home sign) and the semantic relations constructed by two bonobos and a chimpanzee. Seven out of eight of Brown's predominant (1973) universal semantic relations are represented in our corpus and their relative frequency is in the range of human children across cultures for all three apes. The same semantic functions are also expressed at the one-word stage of child language, where children relate their single words to themselves, to gestures, to other people, to objects, and to ongoing action in the present situation (Greenfield & Smith, 1976). In these findings, our data replicate those of Gardner and Gardner, who taught sign language to a chimpanzee named Washoe (B. T. Gardner & Gardner, 1971; R. A. Gardner & Gardner, 1969). Brown

(1970, 1973) and the Gardners (1971) compared Washoe's two-sign utterances to those of human children. Based on a set of six semantic relations (five of which are a subset of the eight discussed above), the Gardners (1971) reported that 78% of Washoe's utterances fell into those six categories. Although we do not know how many of the 294 unique combinations were imitated (Terrace et al., 1979), and how many were spontaneous, the similarity to the spontaneous combinations of Kanzi, Panbanisha, and Panpanzee is striking, as is the similarity to the combinations of children.

In a video study of Washoe and other signing apes communicating many years later, the same basic semantic relations appeared (Rivas, 2005). Rivas, however, claimed that no evidence for semantic relations was found in Washoe's utterances, in direct contrast to the earlier work by the Gardners. Indeed, at this later point in time, the variety of combinations within each semantic relation seemed relatively impoverished in a new environment, with few individual signs being used in many utterances. However, his coding scheme is not completely parallel to ours or other examples of semantic-relation codes; for instance he mentions that some examples of his Action–Object code (e.g., DRINK GUM) seemed more like requesting two items at the same time. In our coding scheme, these relations would have been coded as Action–Entity as the object was not directly acted upon by the action. Therefore, we cannot directly compare our findings to his.

Although a 'true' grammatical rule must use some formal device such as word order to mark the semantic relation, children do not always do this at the two-word stage, even in uninflected languages such as English, whose syntax depends heavily on word order. Some children use word order more consistently than others, but even relatively consistent children show variability both in spoken language (Brown, 1973) and home sign (Goldin-Meadow & Mylander, 1984). There is also variability across the semantic space: out of six relations tested for ordering patterns by Goldin-Meadow and Mylander, the two children for whom the researchers had an adequate corpus of data had an average of four statistically significant ordering patterns for semantic relations created by combining two signs. Matching the deaf children, Panpanzee, a chimpanzee, and Panbanisha, a bonobo, each used lexigrams to construct four semantic relations in a statistically significant order. Kanzi, the other bonobo, constructed only one semantic relation in a statistically significant order; but he acquired his symbol system at a much later age than did Panpanzee, Panbanisha, or the deaf children. The ontogenetic construction of protogrammar is thus similar across the clade.

Nonetheless, as with children, there is also evidence of many lexically based (item-specific) combination rules; for instance, the apes prefer to place the affirmative (YES) first in all of their combinations that include an affirmative (Table 2). However, contrary to Tomasello's (2000) claim for children, it is equally evident that this is not a rote-learned combination, as the apes' caregivers rarely, if ever, make this type of combination. More interestingly, the apes use item-specific combinations in novel contexts. In this case, affirmatives are used most frequently as a request, e.g., YES TRAILER – glossed as something like 'say yes so that we can go to the trailer,' whereas the caregivers, when asking, would never include the affirmative, e.g., they might combine speech and lexigrams to say something like: 'Would you like to GO to the TRAILER?' For all three apes, an indicative gesture plus a lexigram representing an entity could be considered item-based if we consider the deictic gesture as an item. Whether these item-based combinations are the result of a distributional learning process as suggested by Lieven and colleagues, among others, is an interesting avenue for future research (Lieven, Pine, & Baldwin, 1997).

Consonant with the lack of consistent formal marking in early combinations and the existence of item-based constructions across the clade is the concrete semantic nature of these combinations. While important controversies remain, there is broad agreement to the present time that children's language development begins with concrete structures that become increasingly abstract with development (Fisher, 2002; Tomasello, 2000). One aspect of progressive abstraction is the process of grammaticalization. Tomasello (2000) compares the child's grammaticalization (ontogeny) with the grammaticalization that occurs in history (cultural evolution). While our ape data highlight concrete semantic relations as the foundation of symbolic combination, incipient grammaticalization is also a characteristic of the ape corpora. For example, Panbanisha and Panpanzee differentially ordered the meaning relation Action and Goal, depending on whether one communicative element was a gesture or not. From the perspective of syntax, this could be considered a kind of prototransformation, just as passive and active English sentences can express similar meanings with systematically different orderings of semantic elements. Evidence of this kind of complex ordering strategy does not support the strictest version of the Universal Grammar theory of early children's combinations – positing a biologically based Universal Grammar with no roots before the evolutionary split with chimpanzees and bonobos. Instead, evidence for protosyntax in bonobo and chimpanzee suggests earlier phylogenetic roots and a more gradual evolution of syntax in human language.

We also found cross-species similarities in the systematic use of gesture in symbolic combinations (with words in the case of hearing children, with signs in the case of deaf children, and with lexigrams in the case of our two bonobos and a chimpanzee). And, given that language had to be created before it could be learned from a prior generation, we find important evidence in all three species that rules are constructed that are not modeled in the communicative environment (Goldin-Meadow & Mylander, 1984). In terms of the connection between phylogeny and ontogeny, all of these similarities relate to the very early stages of language acquisition in human children, up to about age two. This is very much in line with Bickerton's (1990) idea concerning a simple protolanguage shared by very young children and language-trained chimpanzees.

Differences between the language development of children and apes

Our comparison of the three species also points to distinctions between human children's language acquisition patterns and those of bonobos and chimpanzees. These distinctions provide possible clues as to the pathway taken by the evolution of human language in the last 5 million years. However, an important point to keep in mind is the possible modality confound between children using speech or sign and the apes using the keyboard.

Apes clearly have strong constraints – probably rooted in a smaller brain with fewer neuronal connections – that deter them from progressing beyond the level of a two-year-old child in the arena of grammatical structure. Another apparent difference is that so much of the symbol-ordering structure depends on combining gesture with symbol. While children do this frequently in the second year of life, it is an intermediate stage that they soon replace by combining word with word (Guidetti, 2002; Rodrigo, González, de Vega, Muñetón-Ayala, & Rodríguez, 2004). However, Ozcaliskan and Goldin-Meadow (2005) point out that, for hearing children, gesture–word combinations constitute the leading edge of early language development, leading into increasingly frequent word–word combinations. We can speculate that in phylogeny, as in ontogeny, the use of gesture in this combinatorial way may have been one of the leading edges of language evolution.

One important distinction between humans and apes is in utterance length and the proclivity to combine semiotic elements or morphemes. While bonobos and chimpanzees can combine semiotic elements, they do so much less frequently, and their combinations rarely exceed three elements. In other words, they have clearly not developed complex syntax, such as embedded sentences, relative clauses, or subordinating constructions. In addition, their lexigram and gestural vocabularies remain overwhelmingly concrete. Finally, their use of combinations to inform, rather than to request is much more limited and more infrequent than that of human language users, even young children (but see Lyn et al., 2010). These findings are consistent with those found in sign language-using apes (e.g., Rivas, 2005). Hence, we can conclude that the use of language primarily to inform rather than request, the complexity of symbolic combination, and abstract concepts and vocabulary are all good candidates for the pathway that human language has taken since our divergence from bonobos and chimpanzees 5 million or so years ago.

Still other differences likely reflect the ape way of life in the wild, their specific conditions at the Language Research Center, or specific features of human culture in the US. An example of the former is the frequency of conjoined action constructions such as CHASE BITE and TICKLE GRAB; these are symbolic representations of species-typical play patterns. They of course differ from the play patterns of human children, so the messages they construct about play are different. The YES constructions in contrast reflect the fact that they need to obtain permission from humans for all of their desired actions and objects; Panpanzee and Panbanisha developed the YES construction to ask permission from the human caregivers for whatever they wanted. Finally, the greater frequency of expressing a relation between a possessor and possessed in human children may reflect the importance of possessing objects in US culture and the absence of personal possession in the ape world.

The essence of language is creativity; and all of the constructions that differ from those of humans show that both bonobo and chimpanzee have made the symbol system their own, a creative tool of communication. That brings them much closer to the essence of human cognition than if they had mechanically imitated what humans talk about.

Possible implications for the evolution of human language

While a few animals do not a whole species make, initial small-scale studies of child language development have generally been replicated with larger samples, and our data begin to suggest some language-relevant plesiomorphic traits (traits that are found in all offshoots of a particular common ancestor, suggesting that the ability was also extant in that common ancestor). Data concerning an individual's abilities can only inform us as to the capacity for that ability in that individual's species, not the uniformity of a particular ability throughout that species. Likewise, the capacity for similar communicative abilities in an individual chimpanzee and an individual bonobo cannot definitively indicate the presence of that capacity in their common ancestor, but would be suggestive of at least its potential.

One plesiomorphic (i.e., present in the common ancestor) candidate relevant to language is gestural combination. Gesture has been discussed by several researchers as a possible necessary first step to human language (e.g., Bonvillian et al., 1997; Corballis, 2002). Gesture combinations are not only produced by Kanzi, Panbanisha, and Panpanzee, but they are also found in wild chimpanzees, in untutored chimpanzee colonies, and in human children (Goldin-Meadow & Morford, 1985; Plooij, 1978; Tomasello, 2004; Tomasello, Call, Nagell, Olguin et al., 1994; Tomasello & Camaioni, 1997; Volterra & Iverson, 1995). Most relevant to the present study, a direct comparison of a chimpanzee captive colony with a bonobo captive colony revealed that both species can combine gestures with different contextual elements to construct different messages (Pollick & de Waal, 2007). Additionally, cross-modal combinations (manual action plus visual symbol in our study, manual action plus vocal sound in children and chimpanzees in the wild) are found in all members of the clade (Brown, 1973; Goldin-Meadow & Mylander, 1984; Goodall, 1986; Greenfield & Smith, 1976; Plooij, 1978). Hence, gestural and cross-modal combinations may be part of the clade's language-relevant evolutionary heritage.

Similarly, the capacity to create novel semantic combinations that both follow and depart from ordering patterns found in the communicative environment is a capacity demonstrated by our ape participants of both species, by chimpanzees acquiring sign language, and by human children (B. T. Gardner & Gardner, 1971, 1994). Indeed, the capacity to construct meaningful symbolic combinations may go beyond the *Pan–Homo* clade and extend at least to gorillas (Patterson, 1978) and orangutans (Miles, 1999). However, no direct comparison of these species' symbolic combinations has yet been carried out.

Possible implications for child language acquisition

In recent years, we have learned that while the orderly expression of basic semantic relations appears to be universal and to emerge without a strong model, later stages of complex grammar are less resilient and less universal: in sign language, the size of the signing community, the accretion of complexity over generations, and the age of acquisition are crucial to grammaticalization in the acquisition process (Sandler, Meir, Padden, & Aronoff, 2005; Senghas, 2003). If the potential for combining semiotic elements in a regular way to express semantic relations goes back to the common ancestor of humans, chimpanzees, and bonobos 5 million years ago, then the resilience of the initial crucial steps in human language acquisition becomes very understandable in terms of their depth of evolutionary history. Even between our two 'generations' of symbol-using apes, we can see a progression of protogrammatical construction, with Panbanisha and Panpanzee using lexigrams to order a larger number of semantic relations than Kanzi had.

Conclusions

Our data indicate that the potential for combinatorial communication had already evolved by the time *Pan* and *Homo* diverged 5 million or so years ago. A recent study of gestural communication in colonies of captive bonobos and chimpanzees who have not been taught a humanly devised symbol system has found nonsymbolic analogues to what was found earlier in human children, bonobos, and chimpanzees: the same gesture can combine with different elements to make a different message (Pollick & de Waal, 2007). This provides evidence against the view that our studies have created something *de novo* because of the particular situation of cross-species communication. These data suggest that, while not recorded without human interaction, the foundation for basic productive combinatorial symbolic communication, approximately what a human child does in the second year of life, is present in the two species of our most proximal clade, the bonobos and the chimpanzees.

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Note

1 appendix available at http://fla.sagepub.com/content/31/3/300/suppl/DC1

References

Bates, E., & Goodman, J. C. (1997). On the inseparability of grammar and the lexicon: Evidence from acquisition, aphasia, and real-time processing. *Language and Cognitive Processes, 12*, 507–584.

Bickerton, D. (1990). *Language and species*. Chicago, IL: University of Chicago Press.

Bondioli, A. (2001). The adult as a tutor in fostering children's symbolic play. In A. Geoncue & E. L. Klein (Eds.), *Children in play, story, and school* (pp. 107–131). New York: Guilford Press.

Bonvillian, J. D., Garber, A. M., & Dell, S. B. (1997). Language origin accounts: Was gesture in the beginning? *First Language, 17*, 219–239.

Bonvillian, J. D., & Patterson, F. G. P. (1993). Early sign language acquisition in children and gorillas: Vocabulary content and sign iconicity. *First Language, 13*, 315–338.

Bowerman, M. (1973). *Early syntactic development: A cross-linguistic study with special reference to Finnish*. Cambridge: Cambridge University Press.

Braine, M. D. S. (1976). Children's first word combinations. *Monographs of the Society for Research in Child Development, 41*(1), 1–96.

Brakke, K. E., & Savage-Rumbaugh, E. S. (1995). The development of language skills in bonobo and chimpanzee – 1. Comprehension. *Language and Communication, 15*, 121–148.

Brakke, K. E., & Savage-Rumbaugh, E. S. (1996). The development of language skills in *Pan* – II. Production. *Language and Communication, 16*, 361–380.

Bronowski, J., & Bellugi, U. (1970). Language, name and concept. *Science, 168*, 669–673.

Brown, R. (1970). The first sentences of child and chimpanzee. In R. Brown (Ed.), *Psycholinguistics* (pp. 208–231). New York: Free Press.

Brown, R. (1973). *A first language*. Cambridge, MA: Harvard University Press.

Butcher, C., & Goldin-Meadow, S. (2000). Gesture and the transition from one- to two-word speech. In D. McNeill (Ed.), *Language and gesture*. New York: Cambridge University Press.

Byrne, R. W. (1995). *The thinking ape: Evolutionary origins of intelligence*. Oxford and New York: Oxford University Press.

Corballis, M. C. (2002). *From hand to mouth: The origins of language*. Princeton, NJ: Princeton University Press.

Farver, J. A. M. (1993). Cultural differences in scaffolding pretend play: A comparison of American and Mexican mother–child and sibling–child pairs. In K. MacDonald (Ed.), *Parent–child play: Descriptions and implications* (pp. 349–366). Albany, NY: State University of New York Press.

Fisher, C. (2002). The role of abstract syntactic knowledge in language acquisition: A reply to Tomasello (2000). *Cognition, 82*, 259–278.

Gardner, B. T., & Gardner, R. A. (1971). Two-way communication with an infant chimpanzee. In A. M. Schrier & F. Stollnitz (Eds.), *Behavior of nonhuman primates*. New York and London: Academic Press.

Gardner, B. T., & Gardner, R. A. (1994). Development of phrases in the utterances of children and cross-fostered chimpanzees. In R. A. Gardner (Ed.), *The ethological roots of culture* (pp. 223–255). Dordrecht: Kluwer Academic Publishers.

Gardner, R. A., & Gardner, B. T. (1969). Teaching sign language to a chimpanzee. *Science, 165*, 664–672.

Goldin-Meadow, S. (2003). *The resilience of language: What gesture creation can tell us about how all children learn language*. New York: Psychology Press.

Goldin-Meadow, S., & Morford, M. (1985). Gesture in early child language: Studies of deaf and hearing children. *Merrill-Palmer Quarterly, 31*, 145–176.

Goldin-Meadow, S., & Mylander, C. (1984). Gestural communication in deaf children: The effects and noneffects of parental input on early language development. *Monographs of the Society for Research in Child Development, 49*(3–4), 1–121.

Goodall, J. (1986). *The chimpanzees of Gombe*. Cambridge, MA: Harvard University Press.

Greenfield, P. M., & Lyn, H. (2006). Symbol combination in *Pan*: Language, action, culture. In D. Washburn (Ed.), *Primate perspectives on behavior and cognition* (pp. 255–267). Washington, DC: American Psychological Association.

Greenfield, P. M., Lyn, H., & Savage-Rumbaugh, E. S. (2008). Protolanguage in ontogeny and phylogeny: Combining deixis and representation. *Interaction Studies, 9*, 34–50.

Greenfield, P. M., & Savage-Rumbaugh, E. S. (1990). Grammatical combination in *Pan paniscus*: Processes of learning and invention in the evolution and development of language. In K. R. G. Sue Taylor Parker (Ed.), *'Language' and intelligence in monkeys and apes: Comparative developmental perspectives* (pp. 540–578). New York: Cambridge University Press.

Greenfield, P. M., & Savage-Rumbaugh, E. S. (1991). Imitation, grammatical development, and the invention of protogrammar by an ape. In N. A. Krasnegor, D. M. Rumbaugh, R. L. Schiefelbusch, & M. Studdert-Kennedy (Eds.), *Biological and behavioral determinants of language development* (pp. 235–258). Hillsdale, NJ: Lawrence Erlbaum.

Greenfield, P. M., & Savage-Rumbaugh, E. S. (1993). Comparing communicative competence in child and chimp: The pragmatics of repetition. *Journal of Child Language, 20*, 1–26.

Greenfield, P. M., & Smith, J. H. (1976). *The structure of communication in early language development*. New York: Academic Press.

Guidetti, M. (2002). The emergence of pragmatics: Forms and functions of conventional gestures in young French children. *First Language, 22*, 265–285.

Guidetti, M., & Nicoladis, E. (2008). Introduction to special issue: Gestures and communicative development. *First Language, 28*, 107–115.

Hill, J. H. (1978). Apes and language. *Annual Review of Anthropology, 7*, 89–112.

Iverson, J. M., Capirci, O., Volterra, V., & Goldin-Meadow, S. (2008). Learning to talk in a gesture-rich world: Early communication in Italian vs. American children. *First Language, 28*, 164–181.

Leslie, A. M. (1987). Pretense and representation: The origins of 'theory of mind.' *Psychological Review, 94*, 412–426.

Lieven, E. V. M., Pine, J. M., & Baldwin, G. (1997). Lexically-based learning and early grammatical development. *Journal of Child Language, 24*, 187–219.

Lyn, H., Greenfield, P. M., & Savage-Rumbaugh, E. S. (2006). The development of representational play in chimpanzees and bonobos: Evolutionary implications, pretense, and the role of interspecies communication. *Cognitive Development, 21*, 199–213.

Lyn, H., Greenfield, P. M., Savage-Rumbaugh, S., Gillespie-Lynch, & Hopkins, W. D. (2010). Nonhuman primates do declare! A comparison of declarative symbol and gesture use in two children, two bonobos, and a chimpanzee. *Language and Communication*, doi: 10.1016/j.langcom.2010.11.001.

McCune-Nicolich, L. (1977). Beyond sensorimotor intelligence: Assessment of symbolic maturity through analysis of pretend play. *Merrill-Palmer Quarterly, 23*, 89–99.

Mannle, S., Barton, M., & Tomasello, M. (1992). Two-year-olds' conversations with their mothers and preschool-aged siblings. *First Language, 12*, 57–71.

Miles, H. L. (1999). Symbolic communication with and by great apes. In S. T. Parker & R. W. Mitchell (Eds.), *The mentalities of gorillas and orangutans: Comparative perspectives* (pp. 197–210). New York: Cambridge University Press.

Ochs Keenan, E. (1977). Making it last: Repetition in children's discourse. In S. Ervin-Tripp (Ed.), *Child discourse* (pp. 125–138). New York: Academic Press.

Ozcaliskan, S., & Goldin-Meadow, S. (2005). Gesture is at the cutting edge of early language development. *Cognition, 96*, 101–113.

Parker, S. T., & Gibson, K. R. (1979). A developmental model for the evolution of language and intelligence in early hominids. *Behavioral and Brain Sciences, 2*, 367–407.

Parker, S. T., Langer, J., & McKinney, M. L. (2000). *Biology, brains, and behavior: The evolution of human development*. Santa Fe, NM: SAR Press.

Patterson, F. (1978). Conversations with a gorilla. *National Geographic, 154*, 438–465.

Petitto, L. A., & Seidenberg, M. S. (1979). On the evidence for linguistic abilities in signing apes. *Brain and Language, 8*, 162–183.

Piaget, J. (1962). *Play, dreams and imitation in childhood*. New York: Norton.

Pika, S. (2008). Gestures of apes and pre-linguistic human children: Similar or different? *First Language, 28*, 116–140

Pika, S., Liebal, K., & Tomasello, M. (2003). Gestural communication in young gorillas *(Gorilla gorilla)*: Gestural repertoire, learning and use. *American Journal of Primatology, 60*, 95–111.

Pika, S., Liebal, K., & Tomasello, M. (2005). Gestural communication in subadult bonobos *(Pan paniscus)*: Gestural repertoire and use. *American Journal of Primatology, 65*, 39–65.

Plooij, F. X. (1978). Some basic traits of language in wild chimpanzees? In A. Lock (Ed.), *Action, gesture and symbol: The emergence of language* (pp. 111–131). London: Academic Press.

Pollick, A. S., & de Waal, F. M. B. (2007). Ape gestures and language evolution. *Proceedings of the National Academy of Sciences, 104*, 8184–8189.

Rivas, E. (2005). Recent use of signs by chimpanzees (*Pan troglodytes*) in interactions with humans. *Journal of Comparative Psychology, 119*, 404–417.

Rodrigo, M. J., González, A., de Vega, M., Muñetón-Ayala, M., & Rodríguez, G. (2004). From gestural to verbal deixis: A longitudinal study with Spanish infants and toddlers. *First Language, 24*, 71–90.

Sandler, W., Meir, I., Padden, C., & Aronoff, M. (2005). The emergence of grammar: Systematic structure in a new language. *Proceedings of the National Academy of Sciences, 102*, 2661–2665.

Savage-Rumbaugh, E. S., McDonald, K., Sevcik, R. A., Hopkins, W. D., & Rupert, E. (1986). Spontaneous symbol acquisition and communicative use by pygmy chimpanzees (*Pan paniscus*). *Journal of Experimental Psychology: General, 115*, 211–235.

Savage-Rumbaugh, E. S., Murphy, J., Sevcik, R. A., Brakke, K. E., Williams, S. L., & Rumbaugh, D. M. (1993). Language comprehension in ape and child. *Monographs of the Society for Research in Child Development, 58*(3–4): v–221.

Savage-Rumbaugh, E. S., Sevcik, R. A., Rumbaugh, D. M., & Rupert, E. (1985). The capacity of animals to acquire language: Do species differences have anything to say to us? *Philosophical Transactions of the Royal Society of London, B, 308*(1135), 177–185.

Schlesinger, L. M. (1971). Production of utterances and language acquisition. In D. Slobin (Ed.), *The ontogenesis of grammar: A theoretical symposium* (pp. 63–101). New York: Academic Press.

Senghas, A. (2003). Intergenerational influence and ontogenetic development in the emergence of spatial grammar in Nicaraguan Sign Language. *Cognitive Development, 18*, 511–531.

Stauffer, R. L., Walker, A., Ryder, O. A., Lyons-Weiler, M., & Hedges, S. B. (2001). Human and ape molecular clocks and constraints on paleontological hypotheses. *The Journal of Heredity, 92*(6), 469–474.

Terrace, H. S., Petitto, L. A., Sanders, R. J., & Bever, T. G. (1979). Can an ape create a sentence? *Science, 206*, 891–902.

Terrace, H. S., Petitto, L. A., Sanders, R. J., & Bever, T. G. (1980). On the grammatical capacities of apes. In K. Nelson (Ed.), *Children's language* (Vol. 2, pp. 371–496). New York: Gardner Press.

Tomasello, M. (2000). The item-based nature of children's early syntactic development. *Trends in Cognitive Science, 4*, 156–163.

Tomasello, M. (2003). *Constructing a language: A usage-based theory of language acquisition*. Cambridge, MA: Harvard University Press.

Tomasello, M. (2004). *Social cognition in primates.* Paper presented at the Evolution of Language, Leipzig, Germany.

Tomasello, M., Call, J., Nagell, K., Olguin, R., et al. (1994). The learning and use of gestural signals by young chimpanzees: A trans-generational study. *Primates, 35*, 137–154.

Tomasello, M., & Camaioni, L. (1997). A comparison of the gestural communication of apes and human infants. *Human Development, 40*, 7–24.

Volterra, V., Caselli, M. C., Capirci, O., & Pizzuto, E. (2005). Gesture and the emergence and development of language. In M. Tomasello & D. I. Slobin (Eds.), *Beyond nature–nurture: Essays in honor of Elizabeth Bates* (pp. 3–39). Mahwah, NJ: Lawrence Erlbaum.

Volterra, V., & Iverson, J. M. (1995). When do modality factors affect the course of language acquisistion? In K. Emmorey & J. S. Reilly (Eds.), *Language, gesture and space* (pp. 371–390). Hillsdale, NJ: Lawrence Erlbaum.

Werner, H. (1948). *Comparative psychology of mental development, revised edition*. New York: International Universities Press.

Zukow, P. G. (1986). The relationship between interaction with the caregiver and the emergence of play activities during the one-word period. *British Journal of Developmental Psychology, 4*, 223–234.