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Symbol Combination in *Pan*: Language, Action, and Culture

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When a 2-year-old child says something like "hit ball" (Brown, 1973), the child is implicitly parsing an action event into two constituents, action and object. When a 2-year-old child says something like "Kendall swim" (Bowerman, 1973), the child is implicitly parsing an action event into the constituents of agent and action. Implicit there is an understanding of an agency, Kendall, as instigator of the swimming action. Such linguistic representations are therefore a window into the child's cognitive representation of action. Two related questions that we try to answer in this chapter are the following: Will apes exposed to a humanly devised symbol system parse and represent action events in the way that children do? To what extent are they representing intentional action?

Human children not only use language to parse action events but often do so in an orderly fashion, constructing preferred orders for relating two constituents. An example would be a preference for placing action before object. These ordering tendencies often reflect the language of the child's social environment; for example, verbs before object is the canonical order of English. This raises two more questions: To what extent will apes exposed to a humanly devised symbol system construct preferred orders for expressing action relations? To what extent are these orders cultural (in this case, coconstructed across species lines) rather than species specific?

Yet another question arises in connection with apes whose communicative environment is dominated by their interactions with humans: To what extent

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does the apes' symbolic encoding of action show an awareness of a human state of mind as a prerequisite to ape action?

Whiten et al. (1999) presented evidence for chimpanzee cultural traditions. Most of the evidence presented concerned tool use, but some concerned signaling behaviors. Evidence of this nature makes more likely the possibility that one could see distinct cultural traditions emerging in captivity with regard to communicative behavior. A related question follows: To what extent does any order preference reflect perceived order of a real-world action event as opposed to a cultural norm that is independent of action structure itself?

Communication can itself be looked on as a system of action. Human children (and adults) integrate across two separate modalities: speech and gesture (or, in the case of deaf children, sign and gesture; Goldin-Meadow & Morford, 1985; Goldin-Meadow & Mylander, 1984). From a species-comparative perspective, we may therefore ask to what extent and in what way will apes exposed to a humanly devised symbol system integrate different communicative modalities.

Method

Cladistic Analysis

Cross-species comparisons of bonobos, chimpanzees, and humans permit basic cladistic analysis and provide evidence concerning the evolution of physical or behavioral characteristics. *Cladistics* refers to a taxonomic analysis that emphasizes the evolutionary relationships between different species. A *clade*—the basic unit of cladistic analysis—is defined as the group of species that all descended from a common ancestor unique to that clade (Byrne, 1995). Cladistic analysis separates ancestral traits, which are inherited from the ancestors of the clade, from derived traits, which are possessed by only some of the clade members (Boyd & Silk, 2000). Derived traits arose through natural selection after the divergence of the clade from the common ancestor. Ancestral traits, in contrast, have a genetic (and hence neural) foundation in the common ancestor. Bonobos, chimpanzees, and humans are considered to be a clade that diverged from the common species ancestor 5 million years ago (Stauffer, Walter, Ryder, Lyons-Weiler, & Blai-Hedges, 2001).

By examining behavior in a whole clade, we can use similarities among all three sibling species as clues to what foundations of human language may have been present in our common ancestor 5 million years ago. Such foundations would then have served as the basis from which human language evolved in the following millions of years. Differences among members of the clade would serve as clues to what may have evolved in each species since their divergence 5 million years ago in the case of humans and 2 million years ago in the case of chimpanzees and bonobos (Zihlman, 1996).

In this chapter, we examine the symbolic representation and communication of action information in the clade made up of the bonobo, chimpanzee, and human species. We also examine the role of cultural coconstruction. Although our data came from only 2 bonobos and 1 chimpanzee, the analysis is at the very least an existence proof of cross-species similarities and differences. To complete the clade, we compare our ape participants with the extant literature on human child language.

Participants and Their Communicative Background

Our data came from 2 bonobos, Kanzi and Panbanisha, and 1 chimpanzee, Panpanzee. We compared the symbolic combinations of these apes with the body of empirical research on child language years ago.

Data collection took place at the Georgia State University Language Research Center, under the direction of Duane Rumbaugh and E. Sue Savage-Rumbaugh (Rumbaugh, 1977; Rumbaugh, Savage-Rumbaugh, & Sevcik, 1994; Savage-Rumbaugh, 1986; Savage-Rumbaugh, Shanker, & Taylor, 1998). Ongoing research with bonobos (*Pan paniscus*) and chimpanzees (*Pan troglodytes*) have allowed for some major breakthroughs in our understanding of nonhuman symbol use and cognition.

These bonobo data came from Kanzi, a male born in 1980, and his younger sibling Panbanisha, a female bonobo born in 1985. Panbanisha was raised with her agemate chimpanzee, Panpanzee, who also contributed data to this study. These apes were reared in a communication-rich environment that included English speech, gestures, and lexigrams. *Lexigrams* are symbols on a visuographic keyboard. The symbols are noniconic; that is, they do not in any way resemble their referents—the entities or actions for which they stand. They are arbitrary symbols, their meanings established through the creation of social norms in the Language Research Center. Each lexigram is highly differentiated from all others as a visual pattern. During most of the rearing of these apes, any keyboard presses would result in a computerized voice speaking the English gloss of the lexigram.

Each of these apes used the lexigram keyboard in a symbolic fashion and comprehended their caregivers' use of English at the level of a 2.5-year-old child (Brakke & Savage-Rumbaugh, 1995, 1996; Savage-Rumbaugh et al., 1993; Williams, Brakke, & Savage-Rumbaugh, 1997). At the beginning of the period of the present analysis, May 15, 1989 through October 14, 1989, Panbanisha had a productive vocabulary of about 105 lexigrams. Panpanzee had a productive referential vocabulary of about 70 lexigrams (see Brakke & Savage-Rumbaugh, 1996, Figure 1). They did not use the keyboard randomly, as they had at an earlier "babbling" period. They also had about four spontaneous yet conventionalized gestures.

Data Collection and Data Record

The data from which these findings have emerged came from 5 months of data collection beginning when Panpanzee, the chimpanzee, and Panbanisha, the younger bonobo, were 3.5 years old. Kanzi's data, collected several years earlier, were produced when he was 5.5 years old. All 3 apes were accompanied during the day by humans, who kept a record of every communicative utterance utilizing lexigrams as well as lexigram–gesture combinations.

We focus here on the use of lexigrams and gestures in the combinatorial productions of these 3 apes and in particular, on the two-element combinations of symbol–symbol and symbol–gesture, which were the most prevalent. Presentation of the quantitative data can be found in Lyn, Greenfield, and Savage-Rumbaugh (2006).

All communicative combinations occurred in naturally occurring, everyday situations. The example below shows the information about each utterance that was recorded by a researcher at its time of occurrence:

- Ape: Panpanzee Experimenter: Jeaninne
- Date: 5/15/1989 Combination: True
- Utterance: Apple lexigram + touch gesture
- Code: 714 (request by Panpanzee)
- Context: For more apple to eat, Panpanzee again uses the keyboard to properly ask for the food followed by touching a piece of apple in a bowl. (NOTE: several other foods are also present.)

Here Panpanzee indicated apple on the lexigram board and then touched a piece of apple in a bowl. The ape was noted, as was the experimenter (caregiver) and the utterance itself. The date of the utterance was given, as well as whether that utterance was a combination of two or more elements (the term "true" after "combination" in the entry). A code was assigned to the utterance according to its perceived pragmatic force (request, comment, structured response). Finally, a description was recorded of the context in which the utterance was made. This contextual description is what allowed us to classify these combinations according to their semantic meaning.

Corpora: Nature, Size, and Evolutionary Significance

During this period, Panbanisha had a corpus of 1,088 combinations of two or more elements; Panpanzee had a corpus of 1,000 combinations. Most of the combinations were two elements long (two lexigrams or gesture plus lexigram). After eliminating imitations and other humanly structured combinations, Kanzi's corpus of two-element utterances numbered 723, Panbanisha's numbered 642, and Panpanzee's numbered 637.

These corpora are very large in comparison with most studies of child language and offer rich material for analysis. We note, however, that unlike for children at this age, combinations constituted the minority of the corpus for our animal subjects: 10.4% for Kanzi, 16.7% for Panbanisha, and 16.0% for Panpanzee. Single-lexigram utterances were in the majority; single gestures were not recorded. Our evolutionary perspective on these rates of combining symbols is that they indicate a possible target of natural selection. That is, through natural selection in the human line, symbolic combinations may have gradually become more frequent in the language of human children in the course of the evolutionary process that took place after the divergence of the hominid line from *Pan* 5 million years ago.

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Panpanzee: ***dog*** (lexigram) + ***play*** (lexigram)
agent action

Panbanisha: ***open*** (lexigram) + ***peach*** (lexigram)
action object

Panpanzee: **points to tree** (gesture) + ***play*** (lexigram)
goal action

Figure 19.1. Examples of two-element combinations in the communication of a chimpanzee (Panpanzee) and a bonobo (Panbanisha).

Research Questions and Results

Question 1: Will apes exposed to a humanly devised symbol system parse and represent action events in the way that children do?

Published data on semantic relations of the bonobo Kanzi and the chimpanzee Washoe already indicate that the parsing into two-element relationships is very similar between children and chimpanzees (B. T. Gardner & Gardner, 1994; R. A. Gardner, Gardner, & Van Cantfort, 1989; Greenfield & Savage-Rumbaugh, 1990, 1991). Data from the bonobo Panbanisha and the chimpanzee Panpanzee confirm that the parsing of action sequences into two components is remarkably similar in all three species (Lyn et al., 2006). Examples from Panbanisha and Panpanzee's combinations are found in Figure 19.1.

In the first example (expressing a relationship between an agent and an action), Panpanzee touched the "dog" lexigram (*agent*) and then touched the "play" lexigram (*action*). She then led the caregiver over to the doghouse where Panpanzee and the dogs played together. In the second example (expressing an action on an object), Panbanisha first touched the "open" lexigram (*action*) and then touched the "peach" lexigram (*object*). Her caregiver had just broken a peach. In the third example (representing a goal–action relationship), Panpanzee pointed to a tree (*goal*) and then touched the "play" lexigram (*action*). Her caregiver said "yes" and Panpanzee climbed the tree to play. Here Panpanzee made a request, the predominant pragmatic force for all the apes; implicitly she recognized that her caregiver was an agent who must give her permission to act. Later, we show how both Panpanzee and Panbanisha could make the permission concept explicit through symbolic representation.

All three of the action relationships shown in Figure 19.1 (agent–action, action–object, and goal–action) are among the eight universal semantic relations identified by Brown (1973) in his cross-linguistic analysis of early child language. Indeed, the parsing of action events into representational categories such as action, agent, object, and goal is universal in child language. All of Brown's eight universal semantic relations are represented in our corpus and, in fact, make up the majority of relations in our corpus. These relations are (our terminology in parentheses when it differs from Brown's) agent–action; action–object; agent–object; modifier–head (attribute–X); negation–X; X–dative (X–recipient); introducer–X (demonstrative–X); and X–locative (X–location). (For attribute and negation, X can be either an action or an entity; for recipient, demonstrative, and location, X is always an entity.) All of these categories are also expressed at the one-word stage of child language, in which 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 conclusion, the commonality across the three species in the categories used to parse action and construct action relations is striking indeed. Although we must acknowledge that one animal does not equal a whole species, such structuring of action is highly suggestive. In addition, we are not the first researchers to identify these action structures in the symbolic productions of apes (Brown, 1970). Given that these three species are sibling species, this finding suggests the possibility that the cognitive structuring of action into categories such as agent, action, object, and goal was present before the divergence of *Pan* and *Homo* 5 million years ago. In other words, assuming that these three species are a clade, the findings suggest the possibility that the cognitive structuring of action is an ancestral trait. If this way of parsing action is indeed the foundation of human culture (Bruner, 1990) as well as a building block of human language, then this cognitive structuring of action, as manifest in our common ancestor, would have provided a foundation for the subsequent evolution of both human culture and human language. Consequently, this cognitive structuring of action may have also provided a foundation for chimpanzee culture (Whiten et al., 1999) and even chimpanzee communication in the wild, of which science is relatively ignorant.

Question 2: To what extent are the apes representing intentional action?

In Bruner's (1990) cultural psychology, the categories described above are the foundation of culture, a reflection of our understanding of self and others as intentional agents with goals. Indeed, it is clear that these symbolic combinations are being used to communicate intentional action, both of self and of others. This is particularly evident in examples such as "dog play," above, where the ape expressed what the philosopher of language, John Searle (1979; see also Greenfield, 1980), called *prior intent*, a symbolic expression of a goal-state before the action takes place. In other words, behavior subsequent to the "utterance" made it clear that "dog play" announced a goal-state that Panpanzee intended to achieve.

Such expression of prior intent is present even in the single-word utterances of children (Greenfield, 1980). For example, at 22 months 21 days, a child Nicky (Greenfield & Smith, 1976) said "jump" just as he was about to jump. Here, his word expressed an action goal-state, jumping. From a linguistic perspective, agency was implicit, but from the point of view of the action, agency resided explicitly in the child who was about to jump. Similarly, the apes used their single-symbol productions to signal prior intent; for example, Panbanisha stated "open" at the keyboard and then proceeded to open a backpack.

In the last example in Figure 19.1, Panpanzee made a request, the predominant pragmatic force for all the apes (Lyn et al., 2006); implicitly she recognized that her caretaker was an agent who must give her permission to act. Later, we show how both Panpanzee and Panbanisha could make the permission concept explicit through symbolic representation. At the same time, requests intrinsically involve prior intent. That is, a request constitutes an announcement of an intended goal-state; in this case, the intended goal-state was to play in the tree.

The "apple touch" example with which we started presents another aspect of intentionality. The fact that Panpanzee subsequently ate the apple indicates that the communication was intentional rather than random. At the same time, the presence of alternative foods makes the utterance informative. Indeed, in prior work, Greenfield and Savage-Rumbaugh (1984) established that chimpanzees use their symbols informatively in the information-theory sense of *informative*. That is, they used their lexigrams to select from among available alternatives or to signal change; in contrast, they rarely used them to signal the presence of only one stimulus or to indicate a constant state of affairs (Greenfield & Savage-Rumbaugh, 1984).

Informativeness can include a kind of implicit goal-directedness or intentionality. This type of intentionality is what Searle (1979) called *intention-in-action*. In the "apple touch" example, a linguistic action contained a goal within it: to select from alternatives. This intention-in-action became a means to the partially expressed prior intent: to eat the apple. Human children, like adults, are also informative from their earliest linguistic productions (Greenfield & Smith, 1976). In conclusion, the representation of action relations by apes, like that of human children, is clearly expressing intentional action on the part of an agent. This intentionality incorporates both intention-in-action, as in the expression of informativeness, and the representation of prior intent, as in the expression of a future goal.

Question 3: To what extent will apes exposed to a humanly devised symbol system construct preferred orders for expressing action relations?

All 3 apes constructed preferred orders for expressing action relations (Lyn et al., 2006). One instance is the affirmative–goal relationship (generally a request for an action). In one example, Panbanisha touched the "yes" lexigram (*affirmative*) and then touched the "outdoors" lexigram (*goal*). Her caretaker had just asked her what she wanted to do; she replied with this emphatic request to go outdoors.

This example illustrates the dominant order for affirmative–goal lexigram combinations. Both Panpanzee and Panbanisha showed a statistically significant preference for placing the affirmative lexigram before the goal lexigram rather than vice versa, and Panpanzee showed a stronger preference than Panbanisha (Lyn et al., 2006). This preference, although statistically significant, was not absolute. However, this is true of human children as well (e.g., Bowerman 1973; Goldin-Meadow & Mylander, 1984).

Question 4: To what extent are these relations or orders cultural (coconstructed across species) rather than species-specific behavior?

In this instance, by *cultural,* we mean a kind of microculture coconstructed by a group as small as a dyad; the paradigmatic case and ontogenetic origin is mother–child intersubjectivity (Trevarthen, 1980). We see this kind of co-construction as a social byproduct of a shared environment. Panpanzee, a chimpanzee, and Panbanisha, a bonobo, had the affirmative-goal pattern in common with each other. However, the affirmative-goal relation (let alone the order) was not utilized by either Kanzi or by human caregivers; this is a cross-species (micro)cultural norm that was shared by Panpanzee and Panbanisha only. This finding seems to show the cultural capability for the construction of semantic relations within the genus *Pan*. That is to say, a common environment shared by Panpanzee and Panbanisha was more important than their species difference. In no case did the bonobo Kanzi share a semantic relation or an order preference with Panbanisha, another bonobo, but not Panpanzee, a chimpanzee. Within the limits of the *Pan* genus and symbolic combination, shared cultural environment seems more important than the innate factors associated with species. This particular shared convention, the affirmative-goal pattern, between Panpanzee and Panbanisha helps answer our next question.

Question 5: To what extent does the apes' symbolic encoding of action show an awareness of a human state of mind (intended action) as a prerequisite to ape action?

The apes often used an affirmative to request permission or to emphasize a request. For example: Panpanzee constructed "yes Maryanne" wanting to see Maryanne, or Panbanisha was told that there were surprises at hilltop and she replied "yes hilltop" (asking to go). This usage is not one seen in humans and reflects the social condition under which the apes were raised. A comprehension of their need to request items and to get an affirmative answer from their caregiver allowed for the creation of this type of symbolic combination. This usage also reflects an implicit belief the apes had about the state of mind of their caregivers. They were using language to request a state of permission in their caregivers as well as a lexigram response of "yes" (e.g., yes we can go see Maryanne). In cases of this type, the apes' comprehension of "permission" was reflected in the pause in action following a request until a caregiver responded.

Because theory of mind in chimpanzees is controversial, we might ask what the minimal knowledge of the caregiver and the culture would be for these examples to occur. For example, is it enough for the ape to anticipate the caregiver's behavior? To what extent is it necessary for the ape to understand the human–ape relationship? To what extent does the ape have to anticipate a changed intention? Does the ape have to know something about state of mind? At the very least, it seems that the ape must understand something about human intention-in-action. That is, the ape must know something about the human's goal-directed action. Indeed, we now know from a whole series of experiments that apes do understand intended action (Tomasello, Carpenter, Call, Behne, & Moll, 2005). The ape must also need to know something about the effect of the human's goal-directed action on his or her own action possibilities. It may not be a theory of another mind, but it is knowledge of another's intentional action and of the intersection of another creature's intentionality with one's own.

Question 6: To what extent will symbol order preference reflect perceived order of a real-world action event as opposed to a cultural norm that is independent of action structure itself?

First, note that each relation can be expressed in one of two modalities: by combining two lexigrams or by combining one lexigram and one gesture. Most interesting, the ordering convention for combining two lexigrams to parse and represent an action event is not always the same as the ordering convention for combining lexigram and gesture. Specifically, in the action–goal relation for Panpanzee and Panbanisha, action is usually expressed before goal when the relationship is constructed with two lexigrams. However, goal is generally expressed before action when the relationship is constructed with lexigram and gesture (Lyn et al., 2006).

An example of the lexigram–lexigram order is as follows: Panbanisha touched the "open" lexigram (*action*) and then touched the "dog" lexigram (*goal*). She was asking her caretaker to open the door so they could visit the dogs.

An example of a lexigram–gesture combination is the following: Panpanzee touched the "string" lexigram (*goal*) and then gestured to "go" (flicking her index finger in the direction she wants to go; *action*). Her caretaker said, "Yes, you can go get a string," unsure of what string she was referring to. Panpanzee moved in the direction of the tool room, and a few feet before she got there, bent down to pick up a string from the floor

These two different constructions are analogous in human language to two different surface forms of a similar underlying semantic structure, such as active (agent first) and passive (agent last) forms of the same sentence. These orders do not uniformly conform to the real-world event order: that is, action before goal. Nor do they uniformly conform to the mental order: That is, one must have a goal in mind before undertaking the action that achieves it. Instead, the ordering preferences seem to reflect arbitrary but shared modes of expression. Social sharing is the definition of a cultural norm. The combination of social sharing with arbitrariness is the definition of linguistic convention.

Arbitrary but shared ordering preferences for combining symbols may simultaneously constitute protogrammatical conventions and important aspects of chimpanzee culture.

Question 7: To what extent and how can apes exposed to a humanly devised symbol system integrate different communicative modalities?

All 3 apes combined gesture and lexigram, integrating two communicative modalities. It is notable that they used this particular cross-modal strategy more than their human caregivers did; the latter tended to combine lexigrams with other lexigrams (and with speech) rather than with gestures. The frequency of the apes' cross-modal combinations was in line with a recent consensus at the 2004 Workshop on Gestural Communication in Nonhuman and Human Primates (see Liebal, 2004) concerning the importance of cross-modal integration in the evolution of human language.

Another important point is that all 3 apes adopted the "gesture-after-lexigram" preference as a strategy for accomplishing this cross-modal integration (Lyn et al., 2006). The gesture-after-lexigram strategy was first reported in a study on Kanzi in the absence of any model for this ordering pattern in his human environment (Greenfield & Savage-Rumbaugh, 1990, 1991). It may be a "natural" rule for apes, because both Panbanisha and Panpanzee used it as well; it may reflect Kanzi's enculturating influence on the younger apes; or it may be a response to the importance placed on lexigrams by the humans in this environment. Whatever the reason, this ordering convention is a way of integrating the two modalities in a systematic fashion for communicative purposes. Here are some examples of the use of the lexigram–gesture integration and use of this ordering strategy from Panbanisha's and Panpanzee's corpus. In these examples, they express two different semantic relations, entity-demonstrative and location-entity:

- *Entity-demonstrative*: Panpanzee touched the "monster" lexigram (*entity*) and then the monster mask (*demonstrative gesture*).
- *Entity-location*: Panbanisha touched the "orangutan" lexigram (*entity*) and then pointed to the colony room (*location*), where the orangutans usually were.

Thus, communicative action can in itself be complex because of the cross-modal integration that takes place. Ordering strategies are an effective way to effect such integration.

Conclusions

We have demonstrated that apes exposed to a humanly devised symbol system parse and represent action events in the way that children do, in terms of implicit relational categories such as agent, action, and object. Like children, the apes also use their action representations to express their prior intention to carry out an action (*representation of prior intent*; Searle, 1979) as well as their intention-in-action to select from alternative possibilities. Hence, when socialized to use a symbolic tool, they spontaneously use it to parse action into familiar categories for the pragmatic purpose of expressing both prior intent and intention-in-action. In sum, a crucial underlying component of the action representations of chimpanzee, bonobo, and human child is their intentional or goal-directed nature. The neural foundation for the expression of intentionality may be in the mirror neuron system (Greenfield, in press).

Going one step further in the analysis of intentionality, we note that the use of affirmatives by Panbanisha and Panpanzee to gain permission for a desired action at minimum suggests an awareness of intended human action—the reading of intended action in another creature from another species (albeit a closely related one). It also suggests an understanding of the differential power in captivity of the ape and human—that is, the ape's dependence on the human for resources and stimulation as well as his or her understanding of ape–human power relationship as a prerequisite for ape action. Our data indicate that this explicit awareness increased over time in the community; these conventions (utilizing affirmatives) were shared by the younger apes Panbanisha and Panpanzee but were not used by Kanzi.

Like children, the apes of both species constructed preferred orders for representing particular types of action event. These order preferences reflected both cultural norms (Panpanzee and Panbanisha with affirmative constructions) and genus norms (placing gesture after lexigram). However, the preferred orders do not necessarily reflect the structure of the action itself. For example, an action-goal structure will tend to be expressed with action first when it is a two-lexigram construction but with goal first when it is a lexigram–gesture construction.

With a caveat concerning having only one or two representatives from each species, we note the presence of order preferences in each member of this evolutionary clade. Our caveat is not too strong, because a phenomenon in even one member of a species functions as an existence proof. We also note that all ordering preferences discussed in this chapter are shared across more than one ape and are therefore normative on the microlevel of a dyad or triad. The capacity for arbitrary ordering preferences for combining symbols may therefore be an ancestral trait and so may have existed in the common ancestor of *Pan* and *Homo*. Because we find it to exist in each of the three species, this capacity for arbitrary ordering may underlie the ancestral origins of the autonomous structuring of the representational system, leading ultimately to the arbitrary, yet distinct, linguistic conventions.

Apes exposed to a humanly devised symbol system integrated different communicative modalities into their communicative actions; specifically, they spontaneously integrated gesture and lexigram to express their action representations. This constitutes further evidence for the multimodal nature of human language evolution.

The apes' spontaneous integration of gesture brings up a related matter: Apes utilize gestures much more often than their human caregivers and (probably) more and later than hearing human children. The creativity of the gesture-after-lexigram organization to construct new action relations must not be underestimated; given its prevalence in all three apes, it could be an evolutionary precursor to the combinatorial creativity that is the hallmark of human language

Given that the communication of action information, both in single elements and in combinations, has been observed in the wild in gestures, vocalization, and external visual symbols used by apes (Plooij, 1978; Savage-Rumbaugh, Williams, Furuichi, & Kano, 1996; Tomasello, 1994; Whiten et al., 1999), it is possible that the cross-species commonalities we have identified in combining symbols to express intentional action have their behavioral as well as their neural roots 5 million years ago, before the divergence of *Homo* and *Pan*.

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