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THE EVOLUTION OF HUMAN BEHAVIOUR:
THE RELATIONSHIP BETWEEN
THE BIOLOGICAL AND THE SOCIAL

ABSTRACT: Studies in human evolution, human and non-human primate ethology, behavioural genetics, and neurophysiology ultimately raise the question of man's place in the animal world and his uniqueness. The present paper, based on recent primatological evidence, attempts to demonstrate that many criteria which the anthropologists have traditionally used to prove man's uniqueness can no longer be regarded as true distinctions since most of them are present in apes. The following conclusions were done: 1. Human cultures and those of the chimpanzees are homologous despite the fact that the former are much more complex and variable. The symbolic capacity is man's unique attribute; 2. At present, there are many reliable facts suggesting that representatives of at least one ape species, the chimpanzee, are capable of active learning, imitation, and cultural changes following the accumulation of knowledge under natural conditions; 3. Apes (chimpanzees, bonobos and gorillas) can operate symbols and even create new ones by combining previously known concepts. Captive chimpanzees can spontaneously transmit their linguistic skills to other group members. There is no reliable evidence suggestive of any symbolic information exchange among the apes in the wild; 4. Life histories are highly relevant for understanding behavioural differences between chimpanzees and man. Prolonged childhood and a longer total lifespan resulted in the emergence of unique behavioural strategies, including a longer period of learning, and institutionalized help to mothers; 5. Socioecological data are important for the interpretation of similarities and differences in human and non-human primates. Following certain ecological specialization, human ancestors developed adaptations such as larger group size, and cooperation both within and between groups. Ways and models of hominid's social structure group formation could have been similar to those demonstrated for non-human primate species.

KEY WORDS: Evolution – Behaviour – Culture – Language – Tool-using

INTRODUCTION

Studies in human evolution, human and non-human primate ethology, behavioural genetics, and neurophysiology ultimately raise the question of man's place in the animal world and his uniqueness (Parker, Gibson 1979, Tanner 1987, McGrew 1992, Butovskaya, Fainberg 1993, Picq 1994, Moore 1996). Many anthropologists describe this problem as that of a boundary between animals and man. Archaeologists insist on the tool-making criterion. The problem often reduces itself to unearthing the earliest tool or the earliest bipedal hominid (White *et al.* 1994, Leakey *et al.* 1995). In theological anthropology, the man vs. animal problem is sometimes associated with the idea that the ape is none other than the inverse of man. At the same time, new findings in molecular genetics, primate socioecology, and primate human ethology open up new prospects in revealing our proximity to other living creatures. Direct ethological observations under natural conditions must proceed in close cooperation

TABLE 1. Principal similarities and distinctions between human culture and chimpanzee proto-culture (based on McGrew 1992, Butovskaya, Fainberg 1993, Quiatt, Reynolds 1993, Savage-Rumbough, Rumbough 1993, Whyten, Byrne 1997).

Criteria of culture	Man	Chimpanzee
Non-hereditary transmission of information, both vertical and horizontal	Fully expressed	Documented
Imitation, purposeful learning	Typical in information transmission	Rare, but documented
Social relationships institutionalized, both form and process conventional	Highly expressed	Typical of chimpanzees, and present even in cercopithecines (primates have distinct ideas of relationships with other group members and assess their social status)
Self-recognition	Well developed	Present. Great apes recognize their mirror images as those of themselves and are well aware of their social status and social role
Manipulation of social information	Highly skilful	Capable of using social information and selfishly deceiving others
Capacity for symbolic information transmission (language)	Present in all human cultures	Capable of learning AMSLAN and operate symbols at an elementary level under laboratory conditions. Capable of spontaneously mastering symbolic codes. Information concerning the use of symbols in the wild unreliable.

TABLE 2. Cross-populational differences in wild chimpanzee behaviour which are impossible to relate to ecological differences (after Boesch, Tomasello 1998: 593, supplemented by McGrew 1998).

Behaviour	Populations					
	Bossow	Tai	Kibale	Assirik	Gombe	Mahale
Food–procuring behaviour using tools						
Fishing ants	+	+	–	+	+	–
Extracting honey	–	+	–	–	+	–
Bee fishing with probes	–	+	–	–	–	–
Leaf sponges	+	+	+	–	+	–
Extraction of bone marrow	(–)	+	–	–	–	–
Nut cracking	+	+	(–)	(–)	–	–
Digging termites	–	–	–	–	–	–
Pestle and mortar	+	–	–	–	–	–
Hooked sticks	+	–	–	–	–	–
Chisels	+	(–)	–	–	–	–
Fishing termites	–	(–)	–	+	+	+
Extracting algae	+	(–)	–	–	–	–
Communicative behaviour						
Purposeful throwing	+	+	–	–	+	+
Using branches as dragging	+	+	–	–	–	–
Truncheons	–	+	–	–	+	+
Clasping	–	+	+	–	–	+
Invitation to play	–	+	–	–	+	+
Knuckle tapping	–	+	–	–	–	–
Grooming with leaves	–	–	+	–	+	+
Self-directed behaviour						
Driving away flies	+	+	–	–	+	–
Aimed blow	–	+	–	–	–	–
Ground nest	–	+	–	–	+	–
Leaf napkins	–	–	+	–	+	–
Self-tickling	–	–	–	–	+	–

Notes: + present; (–) absent due to lack of requisite resources; – absent, but not due to the above reason.

with the palaeoethological description of archaeological and fossil remains (Foley Lee 1991, Brugal 1995, Barton 1999, Blurton Jones *et al.*1999). The emergence of a new, specifically human, type of evolution, known as the co-evolution of genes and culture, as well as cultural group selection, have frequently been discussed in this context (Lumsden, Wilson 1981, Boyd, Richerson 1992, Soltis *et al.*1995). The present paper, based on recent primatological evidence, attempts to demonstrate that many criteria which the anthropologists have traditionally used to prove man's uniqueness can no longer be regarded as true distinctions since most of them are present in apes. The following issues will be addressed to demonstrate this:

a) Is human culture homologous to chimpanzee culture? (The latter species was selected as the one especially renowned for its cultural traditions).

b) Are there reasons to believe that chimpanzees and their close African relatives (bonobos and gorillas) are capable of active learning, imitation, and cultural changes following the accumulation of knowledge?

c) Are any signs of symbolic capacity present in chimpanzees, bonobos and gorillas?

d) In what way does the uniqueness of human ontogeny affect man's behavioural characteristics?

e) Can socioecology provide a clue to behavioural differences and similarities between man and non-human primates?

Biological approaches to culture (prerequisites of culture and the notion of protoculture)

Like many other phenomena of human life, certain aspects of culture can be explained from the standpoint of natural sciences (Rodseth *et al.*1991, Eibl-Eibesfeldt, Sutterlin 1992). The most complicated task is to disclose the continuity between primate social structures and human society and to solve certain problems concerning the biological roots of human social institutes and properties such as cognitive abilities, systems for transferring social information, systems of kinship, marriage, and social stratification. The crucial controversy between representatives of the natural sciences and the humanities consists in the fact that the latter usually insist that language was the prerequisite of culture. However, primatologists and physical anthropologists emphasize another point: language is rooted in culture (Quiatt, Reynolds 1995, Dunbar 1997). Our further reasoning will proceed from the second assumption.

The continuity of social life observed between non-human primates and man is critical for understanding the formation of human society in the course of evolution (Butovskaya, Feinberg 1993). The capacity for self-recognition, purposefulness, long-term memory, prediction of others' actions, deception, the understanding of social bonds within the group – these are some, but by no means all, prerequisites of human society, those which are actually observed in great apes.

Some specialists in the "theory of mind" classified the principal features of culture as follows (Whiten, Byrne 1997):

(1) A non-hereditary transmission of information;
(2) Imitation and purposeful learning;
(3) Norms regulating behaviour and regularities in their expression;
(4) Self-recognition;
(5) Manipulating social information (the capacity of predicting and manipulating the behaviour of others, known as Machiavellian intellect).

It would be an oversimplification to deny any differences between humans and great apes in this respect. However, elements suggestive of rudimentary culture are clearly seen in at least one ape species, man's sister taxon: the chimpanzee (*Table 1*). Facts concerning the behaviour of wild and captive chimpanzees indicate that these apes possess most of the above features (*Table 1*). These properties are admittedly by far less developed in them than in man. No reasonable writer would insist that the level of ape culture is anywhere near that of human culture. The question, however, is, in what way these distinctions are due to man's qualitative uniqueness.

A Canadian psychologist (Galef 1992) believes that the principal qualitative distinction of human culture is its capacity for a progressive accumulation of innovations from one generation to another, their progressive sophistication, and further transmission. Over many generations, then, models of behaviour are being formed that a single individual could never have assumed by any non-social interactions. In Galef's view, while chimpanzees, like other animals, have population-specific "traditions", human societies possess what is described as "cumulative culture". This view is based on the fact that instances of actual learning and imitation suggestive of a "cumulative culture" are extremely rare in apes, despite decades of field observations. Galef believes that all behavioural strategies used by chimpanzees can be mastered by individual training. This authoritative writer's ideas are frequently cited by cultural anthropologists who insist that man is unique. Galef himself, however, admits that he had never worked with great apes and would not claim that chimpanzees do not teach other group members, imitate, or accumulate behavioural skills. Moreover, he even suggests that this is essentially tantamount to admitting that the chimpanzee proto-culture may be homologous to human culture (Galef 1998: 606).

Some evolutionary anthropologists, including C. Boesch, a primatologist, and M. Tomasello, a psychologist, point that the understanding of culture hinges upon two types of learning: imitation and emulation. Only in the case of imitation it is possible to speak of a transmission of a specific behaviour, and only imitation is indicative of a cultural tradition. Is this the most important criterion, however? T. Ingold objects by saying that there are no clear distinctions between imitation and emulation since all imitation is emulative. Learning is imitative in

that the novice repeats the instructor's actions; however it is emulative insofar as the skill can be mastered only by prolonged training. The instructor's role, then, consists not in the direct transmission of a skill, but in the creation of a situation under which the novice can master the skill. The distinction between individual innovation and social convention, then, is not crucial.

Clearly, cross-populational differences in behaviour are more pronounced in man than in the chimpanzees. It should be kept in mind, however, that human behaviour appears to be more diverse not only because humans are more widely dispersed, but also because anthropologists have been engaged in comparing cultures for centuries. The Standard Cross-cultural Sample contains relatively complete data on 186 cultures (some 1,700 traits) and Murdock's Ethnographic Atlas accumulates data on 1,267 cultures, although on a smaller number of traits (101). In contrast, naturalistic studies of social behaviour in ape populations have lasted for just several decades. Available data on wild chimpanzees pertain to merely 35 populations (Nishida, Hiraiwa-Hasegawa 1987, Boesch 1990, McGrew 1992, 1998), and field observations on bonobos are even scarcer: two populations of this species at Wamba and Lomako, Zaire (Ihobe 1992, Kano 1992, Hohmann, Fruth 1993).

We will now address cultural differences in tool-use and communication between chimpanzees belonging to six populations, as summarized by Boesch and Tomasello (1998) and supplemented by McGrew (1998) (*Table 2*). The first striking fact that emerges is that behavioural strategies listed in the table are population-specific. They reflect group variations rather than individual differences. For example out of the 123 chimpanzees of the Tai population, virtually all adults were regularly engaged in nut cracking.

It is evident that ecological differences are an important, but not the only, factor underlying cross-population variation in the behaviour of non-human primates. There is ample evidence suggesting that tool-use is practised by some but not all populations of chimpanzees under identical conditions. Cracking cola and panda nuts is a typical example. The tradition is registered in Tai but is absent in most other populations including Gombe, Mahale, various populations of Cameroon, Gabon, and central and western Côte d'Ivoire. Boesch and others have found that the distribution area of this tradition is bounded by the Sassandra-N'Zo River (Boesch *et al.* 1994). Notably, the nut species utilized by the Tai chimpanzees are distributed throughout these areas. Stone tools are universally available, and population densities are comparable.

Population specificity in chimpanzees is much more complex than it may appear at first sight. Traditional behavioural patterns vary across populations in terms of both form and function. Ant digging and leaf clipping are the two most illustrative patterns in this respect (Boesch, Boesch 1990, McGrew 1992). In Tai, chimpanzees hold the stick in one hand and sink it into the mass of soldier ants guarding the entrances to the anthill. After the ants have climbed the stick up to the height of 10 cm, chimpanzees take the stick out and collect the ants with their lips. The average length of a stick in Tai is 30 cm, and it is sunk into the anthill 12 times per minute on average, the mean single catch being 15 ants. Chimpanzees of Gombe, too, procure soldier ants of the same species with a stick. However, the apes wait until the ants have climbed up to the middle of the stick, and only then take it out. After that, they pass the clasped free palm along the tool upside down and rapidly stick the catch into the mouth. Tools are longer in Gombe than in Tai (*ca* 66 cm). The stick is sunk into the anthill 2.6 times per minute on average. The technique used by the Gombe chimpanzees, then, is by far more efficient (760 ants per minute versus 180 in Tai). These two techniques illustrate marked differences between cultural traditions. Members of each population use their own technique and master it by learning and imitation.

While food-extracting strategies may, at least partly, be due to actual or past ecological differences (however small these might be), facts concerning tool-use for communication or self-directed behaviour do not yield themselves to similar interpretations. These differences may only be explained by social factors (*Table 2*).

Leaf clipping as a communicative signal has been described in several populations. Chimpanzees grab a leaf near the base and pass it to and from between their teeth separating parts of leaves with their incisors. The action produces a loud ripping sound. Leaves are not eaten. The function of this behaviour is purely communicative. Its communicative content varies from one population to another. This behaviour was regularly observed in Mahale, Bossow, and Tai. Its context is especially noteworthy. In Mahale, it is used for attracting a sexual partner, in Bossow, for relieving frustration or in a play context. In Tai, leaf clipping was performed only by males, as a prelude to drum roll (Nishida, Hiraiwa-Hasegawa 1987, Boesch 1995).

All the population differences described above result from social rather that individual learning triggered by local ecological conditions. Not only can specific behaviours be present or absent; moreover, their forms and functions, too, vary across populations. This evidently attests to an appreciable role of social environment in the formation and development of population-specific behavioural models in chimpanzees and reveals some basic similarities between their "protoculture" and human culture (Boesch, Tomasello 1998).

Gender differences in traditional human cultures and sex differences in the behaviour of non-human primates

Cultural and social differences between classes of individuals are quite typical of humans, gender differences being among the most expressed. Indeed, in most traditional cultures, each age-and-sex group has its own rites or dances, and the sexual division of labour is a characteristic feature of human economy. In contemporary hunter-gatherer societies, men and women normally perform different tasks: men mainly hunt large game although women may be engaged in fishing in considerable amount of cases in some hunter-gatherer societies, and women collect plants, prepare food and take care of infants. Gender differences, however, are not a unique feature of man, some of them are found in non-human primates. In chimpanzees, hunting is practised nearly exclusively by males, whereas collecting insects such as wasps is often a female prerogative. Sex differences in insectivory were observed in different localities, and females were always more active insect collectors than males. In contrast, males, unlike females, tend to form hunting parties (Tai, Gombe) and are more successful hunters. Gender differences in hunting activities cannot be due to the females' inability to hunt. If females join male hunting parties they can be equally successful in capturing prey, but they seem to avoid doing that. Males, too, are normally able to fish ants and termites. The sex differences in foraging strategies may have evolved due to a number of factors (McGrew 1992): (1) Males are larger, stronger and better equipped for hunting compared to females; also, hunting is less energy-consuming in males, and they are less vulnerable if counterattacked by the prey; (2) Insects are less costly to acquire, and constitute a more reliable and localized food resource; it is more advantageous for females to specialize in insect diet; (3) Because males travel more than females do, they have more chances to detect prey; (4) In the case of males, it is less likely that the prey will be taken away by dominants; (5) Because males do not need to carry infants, they move faster and are more successful hunters. It is more advantageous for the females to fish termites because infants can play, rest and suckle while females are concentrating on fishing.

Also, certain sex differences in communication were found. In Tai, for instance, all adult males practice leaf clipping, whereas no female was observed to do that. Like in human societies, gender stereotypes may vary across chimpanzees populations. While termite fishing is mostly a female occupation in Gombe, all adult individuals practice this skill in Kasakela. It is not known which factors were the most important in the evolution of sexual division of labour in the human lineage, but field observations concerning chimpanzees indicate that sex differences in foraging and other daily activities are not necessarily linked to increase in brain size or longer infant dependency (Boyd, Silk 1997). Economic cooperation between the sexes may be rooted in small-scale sex variations in subsistence strategies and may become a beneficial strategy in the course of human evolution.

How do new behavioural models evolve in populations?

A novel behaviour may spontaneously emerge in a population; alternatively, it can be introduced by immigrants from other populations. Theories of cultural evolution suggest criteria predicting which of the new behavioural models would survive and which would decline; also, they describe the ways in which new traditions can replace old ones (Boyd, Richardson 1993, Durham 1991, Lumsden, Wilson 1981). The distribution of specific cultural invariants in human population is not random since the outcome is affected by a number of restrictions. The analysis of primatological data suggests that the same applies to primate populations. The spread of potato-washing habit in the Koshima macaque population was due to the fact that Imo, a young female who had invented the habit, communicated mostly with her matriline members. Understandably, the custom spread among these specific animals since members of other matrilines had less chances of observing this behaviour. What we see, then, is social restriction.

Can one trace any substantial differences between the social restriction processes in man and non-human primates (great apes in particular)? In human society, two types of restrictions regulating the distribution of cultural skills have been described: social norms and social models. The choice of a cultural invariant directly depends on what the group members see. The distribution of a novel behaviour may be based on free choice, convention, or imposition. Under the condition of a free choice, any innovation has equal chances to be fixed in the group, and group members are tolerant to innovations. If so, the diversity of cultural variants is limited only by the frequency with which innovations emerge within a group and the probability of their introduction from outside. If innovations are controlled by a convention, then group members tend to be intolerant to everything novel. Any new behaviour is immediately rejected and is no longer practised. Such convention is exemplified by the practice of ant fishing in Tai and Gombe. Although the Gombe technique is more efficient, the Tai population strictly adheres to its own tradition without adopting or imitating any innovations.

Imposition is a process whereby a group forces its cultural traditions upon another one. In this case, cultural evolution basically turns into a political process (Durham 1991). Human society abounds in such examples. Imposition may be practised by informational expansion (dissemination of knowledge and skills). Westernization and global unification of certain behavioural models in our days suffice to illustrate this form of cultural transmission. In chimpanzee societies, rudimentary "imposition" assumes the form of manipulation, such as that to which the nut-cracking skill is subjected in Tai.

Being restricted by cultural norms, individuals select those cultural practices which are used by other group members. Some types of cultural behaviour are evidently profitable for the performers, and if they spread throughout the population, one might speak of adaptation as a factor in the choice of the specific group tradition. However, there are numerous examples demonstrating that less adaptive modifications can be chosen as cultural models. In human society, this is illustrated by phenomena such as the feud,

the fertility fall in industrial countries due to the spread of contraceptives, infanticide, smoking, and drug addiction. Chimpanzee parallels include an already mentioned less efficient technique of termite fishing in Tai.

Ways in which maladaptive and selectively neutral cultural behaviours spread in human and chimpanzee populations are similar. Culture-specific modifications appear randomly and the process resembles the genetic drift in evolution (Soltis *et al.* 1995). Boesch and Tomasello (1998) describe five models limiting the distribution of cultural variants: individual, family, group, majority, and prestige. Under the individual model, individuals have free choice and may adopt any behaviour that would maximize their individual fitness (Durham 1991). Under the family model, individuals are tightly associated with their kin and adopt only those models that are practised by their kin. Because cultural changes arise and spread within family lineages, social differences within a group may be quite marked. The family model provides an example of a system with vertical inheritance. In the traditional version, knowledge is being transmitted from the mother to her children, but a new skill may be adopted another way round. In Japanese macaques, the elder individuals acquired the potato-washing habit from the infants, whereas the young animals learnt it observing their peers (Kawai 1965).

In the association model, the transmission of cultural practices is directly related with the network of social relationships. Similar cultural practices are observed in individuals who communicate with each other most often. In cercopithecines, the association is higher within matrilines (in this situation, the family model and the association model function similarly). In chimpanzees, association and kinship are less tightly linked, and the two models behave differently.

In the majority model, individuals select behaviours practised by most group members. Various cultural models may coexist within a population, but that practised by most is the preferred one. Under such conformism, any innovations will meet considerable resistance.

In the prestige model, individuals adopt behavioural strategies from those group members whom they consider the most prestigious. This provides some chance for within-population diversity since each individual is free to choose his/her own model for imitation. The criteria of selection are socially determined. Low-ranking individuals tend to imitate high-ranking ones (as in chimpanzees), and young ones copy the behaviour of elder and more skilled ones (this is the way in which hunting skills are acquired in hunter-gatherer groups).

Social norms and social models often exert a joint effect on behaviour. Restrictions at both levels have the same effect: they reduce the rate of social change. Within a single population, the model practised by the majority hampers any alternative food-procuring strategies. The prestige model is the least restrictive one in terms of greeting behaviour, and under the individual model a greater variation of feeding calls is possible. Within a population,

certain changes will be rapid whereas other will be quite slow. This demonstrates that the rate of behavioural changes cannot be regarded as the crucial feature of culture.

Cognition and language as criteria of human uniqueness

The most important issues in understanding similarities and differences between human and ape behaviour are those of cognition and language, and the rudiments of these capacities in animals (Piaget 1951, Vygotsky 1962). The study of human ontogeny makes it possible to trace the development of the modern human mind but is of little relevance for phylogenetic reconstructions (Lock 1993). Modern man's life history differs from that of the great apes. Specifically, adult mortality is lower, fertility is higher (although the reproductive span is comparable to that of the chimpanzee), the inter-birth interval is shorter, the reproductive period starts later, and childhood is much longer (Blurton Jones *et al.* 1999). Because these changes occurred over several millions of years of hominid evolution and are quite considerable, the analysis of the modern child's mental development provides no direct clues as to the phylogeny of the mind. If capacities of human and chimpanzee infants are compared, it is evident that differences in the timing of locomotion bring about very different modes of object exploration (Lock 1993: 294). While chimpanzee infants approach the object quadrupedally and grasp it with their lips, children must first grasp the object with their hands and then put it into the mouth. This sequence (hands followed by the mouth) is typical of the child and is not preceded by a stage described in chimpanzee infants. No wonder that the further development of object manipulation, too, is different. According to Langer, "logical (classifying) and physical (causality) cognition develop in parallel in children, second-order cognition develop by the second half of infant's second year, when symbolic and linguistic production begins to be substantial" (Langer 1993: 310, 312). Thus, being genetically so similar, chimpanzees and humans demonstrate evident behavioural differences rooted in their ontogenetic programs.

The basic factor in the development of man's cognitive abilities is prolonged childhood and adolescence. In this respect, again, man's ontogeny is radically different from that of the chimpanzee. The syntactic capacity develops gradually, on the basis of the need for a rapid procession of word sequences. In the course of evolution, following the increase in general intellectual level and the increased need for the transmission of complex information concerning past events or plans for the future, communication was becoming progressively less dependent on the direct context. The huge intellectual gap between chimpanzees and man thus results from learning rather than from innate biological differences.

An innovation such as speech could have caused rapid evolutionary changes. Language was being mastered by cultural transmission and was a powerful selective factor

stimulating biological changes. Community members who, for some reasons, had been unable to acquire this efficient communication means, became isolated from others.

Experiments in teaching language to chimpanzees, bonobos and gorillas, conducted since the early 70s, have provided important evidence regarding the cognitive capacities of the apes. These capacities suffice for mastering the principal linguistic structures. Despite numerous objections put forward by the sceptics, it has become evident that apes need not be trained in a forcible manner since they spontaneously and actively stimulate the learning process. Bonobo infants Kanzi, Mulika, and Panbanish were able to acquire a large vocabulary and handle symbols in an adequate manner by listening to their teachers and observing them, just like human infants do in normal families. Kanzi and his siblings themselves selected those symbols which they wished to master, and the selection process was individual since their vocabularies were not identical despite considerable overlap. While the first words acquired by Kanzi were "orange", "peanut", and "banana", the first ones learnt by Malika were "milk", "room" and "surprise", and those mastered by Panbanisha, "milk", "open", and "tickle" (Savage-Rumbaugh, Rumbaugh 1993: 91). Bonobos have learnt to associate spoken words with their referents, and only after that did they begin to link words with geometric symbols. At the age of five, Kanzi was able to understand human speech without training, using ear-phones, and to correctly select the referents on photos. At the age of six, Kanzi was capable of an audial identification of 150 words and even showed some understanding of a synthesized speech (although with less success than with real speech).

It has been demonstrated, then, that apes are able to separate single words in the speech stream and recognize their phonemic components rather than focusing on the speaker's intonation and stresses in an intuitive manner. At the age of five, Kanzi differentiated between various concepts and displayed a syntactic ability. Also, he correctly perceived the word order and displayed an adequate reaction to reversals in word order. The comparison of correct answers given by him and Aliya (his educator's two-year-old daughter) demonstrated that in cases where reverse word order was to be followed by a different action, Kanzi suggested correct solutions more often: 80% versus 63% (Savage-Rumbaugh, Rumbaugh 1993: 97).

At present, the longest inter-specific communication project based on the American Sign Language and headed by F. Patterson, involves three gorillas (Koko, Michael and Ndume) and has demonstrated an enormously high level of intelligence in this species (Patterson 1986). So far, the gorilla named Koko has a working vocabulary of over 500 signs. She is able to construct 3–6-word-long utterances and usually initiates conversations with humans. The project has demonstrated the presence of most aspects of human behaviour (although in a less developed form) in gorillas. Findings made at the Chimpanzee and Human

Communication Institute, Central Washington University, are highly relevant for the intelligence of gorillas, chimpanzees, and bonobos, suggesting that the transmission of verbal skills in apes may follow the family model. The chimpanzee named Washoe began to teach her infants AMSLAN quite spontaneously.

Experiments in teaching language to apes demonstrate that chimpanzees, bonobos and gorillas have cognitive capacities sufficient for language acquisition and, provided an adequate social environment, these capacities can be realized. The idea that language evolution is related to the tool-using behaviour appears self-evident to the anthropologists. Recent studies have drawn our attention to another important prerequisite of language: the complexity of social environment. It is important to realize the complex nature of the intelligence phenomenon. "Machiavellian manipulation, cognitive mapping, extractive foraging and technical skill" might play the role of selective pressures on different stages of human evolution, and in most cases these factors were acting together (Byrne, Whiten 1997: 17).

Socioecology as a source of unique species-specific adaptations

A complex social environment requires a sophisticated communication system, and the same environment secures the preservation and transmission of tool-using traditions in a community. Other things being equal, species living in larger groups tend to possess a more developed tool-using capacity and a more complex communication system compared to other closely related taxa. The important factor in the development of cognitive abilities is nutrition. Socioecologists were the first to have recognized the relationship between types of nutrition and relative brain size (Clutton-Brock, Harvey 1980, Foley, Lee 1991).

Results of a multiple regression analysis based on 68 independent parameters taken from the main primatological database (119 species) suggest that brain size is independently and positively correlated with the proportion of fruit in the diet and with the size of the social group (Barton 1999: 170). On the other hand, the ontogeny imposes certain restrictions on the development of the mammalian brain by limiting the variability of certain areas (Finlay, Darlington 1995). The prolongation of childhood results in the development of evolutionary younger brain structures. It is not incidental that larger brains of primates, as compared with those of the insectivores, go along with a relatively large neocortex (Barton 1999: 176).

The adaptive specialization of the brain proceeds in a specific direction. Diet is correlated with sensory structures. In diurnal primates, for example, frugivorous taxa have a larger primary visual cortex, especially the parvocellular visual pathway, than have the folivorous ones. Among the nocturnal taxa, olfactory bulbs and piriform lobes are enlarged (Barton *et al.* 1995). The evolution of colour vision that had occurred in frugivorous primates affected the neocortical growth. In haplorhine primates, the

development of the visual channel is correlated with the development of complex social systems (Allman 1987: 639). Frugivory, then, has contributed to the evolution of social intellect and symbolic capacity, although in an indirect manner. Common ancestors of chimpanzees and humans were apparently frugivorous and their brains were affected by the above-mentioned changes.

Specialization that had ultimately resulted in the emergence of spoken language would have been impossible without the high level of cognitive abilities and a propensity for manipulatory and tool-using activities (technicall skills used in foraging provided the requisite basis).

According to some writers (Byrne, Whiten, 1992), the anthropoid clade has undergone selective pressures favouring greater Machiavellian intelligence. This produced a higher capacity for learning and using social knowledge, and resulted in the increase in brain size, primarily the neocortex (Dunbar 1992). It was demonstrated that a positive correlation exists between neocortex size and group size, thus the large neocortex could serve as an indicator of selection favouring social intelligence (Barton, Dunbar 1997). Life in social groups makes gentle social manipulation, as compared with overt conflict, more advantageous both for the participants and for other group members. For example, female baboons who engage in sexual contacts with young males can avoid the alpha male's interference by staying behind the whole group and inhibiting loud copulation calls or by quietly travelling in an atypical manner (as do Ateles females who, in this situation, quietly walk on the ground despite belonging to a typically arboreal taxon).

Deception strategies are much more sophisticated in apes than in monkeys. Great apes, unlike monkeys, demonstrate the understanding of deception as a means of social manipulation. The development of social deception, typical of species with a complex social structure and intense social life, may be viewed as an important means of coping with social tension. Cognitive capacities of lower catarrhines (for example, of hamadryas baboons) evidently suffice for using specific forms of social manipulation aimed at restoring bonds between former opponents in situations where direct reconciliation is difficult for some reasons (for instance, where difference in status is consideraole and a subordinate is afraid to approach the dominant). The behaviour of a hamadryas female after a conflict with another female from the same harem is an example. The target immediately "complains" to the male and, after having received support from him, sits down on his side and begins actively grooming him. The female who initiated the conflict sits down on the opposite side of the male and does the same. After a while, both females move closer together and eventually begin grooming one another while the male goes away.

Common ancestors of humans and chimpanzees apparently possessed all the prerequisites for the emergence of language. Subsequently, after the two sister taxa had diverged, their adaptations followed different paths. Human ancestors specialized in the direction of larger communities, intensified social life, and social coordination. The transition to life in an open habitat required a more sophisticated communication system which made collective hunting and group defence more efficient and made the hominids adaptively superior to the carnivores.

Also, variations in brain size are associated with the energetic cost of gestation and lactation (Martin 1996). Martin has revealed significant correlations between brain size, metabolic rate and gestation length for 53 mammalian species.

Ontogenetic changes resulted in another unique feature of man: the menopause. Prolonged childhood and the related helplessness of infants resulted in the mothers' much greater dependence on other group members. Until recently, it was believed that the solution was mainly provided by males (fathers). However, according to a hypothesis put forward by Blurton Jones, Hawkes and O'Connell (1999), grandmothers may provide more efficient aids. In modern hunting-gathering and early agricultural societies, both matrilineal and patrilineal, maternal grandmothers often provide grandchildren with the larger share of vegetable food. Also, they assume care of elder children.

From the standpoint of evolutionary psychology, then, menopause makes sense in that it contributes to the viability of the species. Elder women have less chances of raising their own children because of the increased likelihood of death; however they can enhance their inclusive fitness by taking care of their grandchildren.

Socioecology and social structure

Modern humans are known to possess the highest interpopulational differences in social structure compared to non-human primates. Are these differences in any way associated to socioecology? Primatological evidence apparently gives a general answer to the question. According to the socioecological paradigm, the degree of complexity of social relationships and social mechanisms aimed at preventing social tension depend on the context in which the species exists (Sterck et al. 1997). The species, then, is regarded as one of the components of a local ecosystem, whereas social relationships are viewed as factors optimizing the adaptation of groups within this species to the respective ecosystem. Social relationships are an outcome of ecological pressures on individuals, and social behaviour is aimed at enhancing inclusive fitness, which is different in males and females (this rule applies to the human species as well). Food is the main factor limiting females' reproductive success, whereas the males reproductive sucess is supposed to be limited by the access to females (Wrangham 1980).

Between-group contest is regarded as the primary stimulus for female bonding because its effect on the fitness of females is supposed to outweigh the effect of within-group competition. Although females may form groups to reduce the risk of predation and, in the process of group formation, within-group competition for food may arise

(van Schaik, 1989). Wherever food is easily monopolized, within-group competition is of the contest type and female relationships are despotic and nepotistic, resulting in a female-bonded group structure (van Noordwijk, van Schaik 1987, van Schaik 1989). In situations where food resources are scarce and dispersed, competition is of the scramble type, as in Saimiri spp. (Mitchell et al. 1991) and non-female-bonded groups are likely to emerge. Competition between females is virtually absent where resources are abundant and distributed over large patches, as in Presbytes thomasi (Sterck et al. 1997). In such cases, relationships between females will be egalitarian and dispersive, and a non-female-bonded group structure is highly probable.

Female-bonded or non-female-bonded groups are formed mainly because the effect of within-group contest is generally more important than that of between-group contest.

Many non-female-bonded species are folivorous, one example being Gorilla gorilla beringei (Watts 1994), whereas most female-bonded ones are frugivorous (Macaca spp., Schaik 1989, Butovskaya 1993). In situations where animals feed basically on large fruit trees and supplement their diet with other types of food, within-group competition may be low. In contrast, the likelihood of between-group competition may be high and a female-resident pattern can be expected (Erythrocebus patas) (Chism, Rowell 1986).

Van Schaik's model mentioned above mainly explains the reasons underlying group formation in females. Later, it was attempted to predict social relationships in males (van Hooff, van Schaik 1994). Because females, who are the limiting resource for males, cannot be easily shared, it was predicted that cooperation among males is less common and mainly takes the form of reciprocal altruism and cooperative alliances.

Explanation of the evolution of female grouping in primates requires the understanding of the feedback in the evolution of social relationships (Sterck et al.1997). One of the catalyzing stimuli is the infanticidal strategy of males which must certainly have affected female strategies in species where infants were endangered. The risk of infanticide can promote the formation of multi-female, multi-male groups. This is due to the fact that within such social structure, females can make paternity less certain (by failing to display external signs of ovulation, by promiscuous matings, etc.) thus ensuring a multi-male protection for their infants. Infanticide risk may be the fundamental reason for grouping in situations where predation risk, within-group contest and between-group contest are low (Sterck et al. 1997). The comparison of congeneric species (those of the genus Macaca, for example) has revealed that patterns of coping with social tension are less developed in more arboreal species compared to more terrestrial ones. This is due to a greater importance of sociality for the survival of single individuals in terrestrial species, where group life provides a defence against predators and an access to resources under competition with conspecific groups.

The prerequisite of an efficient social structure is a positive balance between a individual cost and the benefit which sociality provides to a single individual. This balance may vary across conspecific populations, ultimately resulting in the emergence of between-population differences in dominance style and, respectively, in various behavioural models aimed at preventing social tension and removing its effects.

Phylogeny and the similarity in social organization

Sometimes, however, the variation of social strategies cannot be ascribed to ecological factors and phylogeny is a major determinant of social relationships (Thierry 2000). This hypothesis seems to account for the main patterns of social organization in the genus Macaca (Thierry 2000). According to the 4-grade scale of social organization proposed by Thierry, dominance styles and patterns of social activity are distributed from rigid to relaxed egalitarian. Macaca mulatta and M. fuscata belong to grade 1, being the most nepotistic species with largely asymmetric and dictatorial relationships (Butovskaya 1993, Thierry 1985, 2000). Low-ranking individuals always keep an eye on the alpha male (this is the essence of the attention structure phenomenon), try to please him, and avoid direct competition with him for food or sexual partners. They must demonstrate submission to the alpha male in order not to be attacked by him. Grade 2 species, represented by Macaca fascicularis and M. nemestrina, are similar to those of grade 1 in terms of social patterns, but all the distinctive features of this grade are less expressed. Grade 4, represented by Macaca tonkeana and M. nigra, exhibit the most symmetrical and egalitarian social relationships (Thierry 1985, Matsumura 1999). Grade 3, which includes M. arctoides, M. assamensis, M. radiata, M. thibetana, etc., is similar to grade 4 by having mild social relationships, high-ranking animals being interested in maintaining relationships with the subordinates (Butovskaya 1993). In both grades 4 and 3, the overall affiliation level within the group is high, subordinates enjoy greater freedom and can themselves initiate contacts with the dominants. For example, a typical pattern used by the dominants to neutralize aggressive motivation of subordinates is ritual biting, and injuries are rare.

The reconctruction of the ancestral state of macaque social organization on the basis of empirical data revealed that M. sylvanus, M. silenus and M. arctoides (grade 3 species) are the closest to this condition (Thierry 2000). The conclusion is supported by morphological and genetic data, at least for M. sylvanus and M. silenus since both are close to the reconstructed ancestral macaque (Cunnigham et al. 1998). The radiation of macaques might have occurred in three waves, and in the course of divergence, differences in dominance styles became extreme (despotic vs. egalitarian) (Matsumura 1999). The Macaque Model of social evolution seems to be relevant for the understanding of the origin of different social systems in humans.

Group life history and social organization

In certain cases, group differences in social organization can hardly be attributed to feeding ecology or population density. The problem that arises is that of the individual components in the formation of a social style and tension regulating strategies. Relationships within a group largely depend on group history and the characteristics of single individuals (Datta 1989, Butovskaya 1995). Our observations on two groups of long-tailed macaques may serve as a good model. Differences in dominance style that we have found between two groups of *M. fascicularis* approach the inter-specific differences in magnitude. The two groups were kept in cages under identical conditions. Their diet, too, was identical. The groups consisted of eight and ten adult animals, respectively, and each one included an alpha male. The crucial difference was that one of the groups (group H) consisted of animals which were high-ranking by birth, while another one (group L) comprised only those whose mothers were low-ranking (Butovskaya, Kozintsev 1996).

Values of Landau's index indicated that the hierarchical structure in both groups was moderately linear. However, nearly all parameters of aggressive behaviour were significantly higher in group L, with the sole exception of injury rate. Reconciliation in group H was very rare, and victims seldom redirected aggression to other individuals. Also, they rarely sought consolation from the third parties. The alpha male in group H was virtually the only animal who comforted the victims after aggression.

Female aggressors in group L initiated reconciliation seven times more often than did their counterparts in group H. In group L, victims sought contacts with their friends, who soothed them, nine times more actively than did victims in group H. While ritual biting was fairly common in group L, it was almost never practised in group H (Butovskaya, Kozintsev 1996). In terms of dominance style, group H may be described as a community of a despotic type, and group L as an egalitarian one. The two groups can be regarded as a model for the evolution of various dominance styles and various mechanisms of coping with social tension under identical ecological conditions (Butovskaya, Kozintsev 1996). Thus, conspecific groups can display marked differences in dominance style and can use various ways of regulating social equilibrium not only due to differences in ecological conditions, but due to different group history, and unique personalities of group members.

Despite the extreme variability of human social systems, ways and models of their formation could have been similar to those demonstrated in non-human primate species (all factors, including phylogeny, socioecology, and group history, being considered).

CONCLUSIONS

(1) Human cultures and those of the chimpanzees are homologous despite the fact that the former are much more complex and variable.

(2) At present, there are many reliable facts suggesting that representatives of at least one ape species, the chimpanzee, are capable of active learning, imitation, and cultural changes following the accumulation of knowledge under natural conditions.

(3) Apes can operate symbols and even create new ones by combining previously known concepts. Captive chimpanzees can spontaneously transmit their linguistic skills to other group members. There is no reliable evidence suggestive of any symbolic information exchange among the apes in the wild.

(4) Life histories are highly relevant for understanding behavioural differences between chimpanzees and man. Prolonged childhood and a longer total lifespan resulted in the emergence of unique behavioural strategies, including a longer period of learning, and institutionalized help to mothers.

(5) Phylogenetical and socioecological data as well as group history are important for the interpretation of similarities and differences in social organization of human and non-human primates. Ways and models of hominid social structure formation could have been similar to those demonstrated in non-human primates.

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