

# What Makes Us Human (*Homo sapiens*)? The Challenge of Cognitive Cross-Species Comparison

Christophe Boesch

Max Planck Institute of Evolutionary Anthropology

Two major theoretical approaches have dominated the quest for uniquely human cognitive abilities: a developmentalist approach stressing the importance of environmental and social conditions, and a predominant approach in experimental and comparative psychology, the deterministic approach suggesting the effect of environmental and social conditions to be minimal. As a consequence, most claims of human cognitive uniqueness are based on comparisons of White middle class Westerner humans (*Homo sapiens*) with captive chimpanzees (*Pan troglodytes*). However, humans are much more than only White middle class Westerners, and chimpanzees are much more than only captives. A review of some data available on different populations of humans and chimpanzees reveals that only the predictions of the developmentalist approach are supported. In addition, systematic biases are too often introduced in experiment protocols when comparing humans with apes that further cast doubts on cross-species comparisons. The author argues that only with consideration of within-species population differences in the cognitive domains and the use of well-matched cross-species experimental procedures will an objective understanding of the different cognitive abilities between species emerge. This will require a shift in the theoretical approach adopted by many in experimental and comparative psychology.

*Keywords:* human, chimpanzee, comparison, within-species variation, cognition

Humans (*Homo sapiens*) have always been interested in “what makes us human” and “what distinguishes us from other animal species.” In all traditional societies, myths have been proposed that provide scenarios as to how humans came to be and of a possible relationship with other animals. Religion and science have zealously taken up the challenge and have come up with their own propositions. Originally, most scientific propositions about human origin did not rely on observations from other species, simply because information on these species was not available. For example, culture was proposed in the early 1930s to be a uniquely human ability before any relevant data on different animal populations were available (Barnard, 2000; Kuper, 1999). Similarly, claims about uniquely human abilities to use and make tools were proposed in the late 1880s, well before observations on wild primate populations (Bowler, 1989; Darwin, 1859).

Since the early 1960s, field observations on the natural behavior of many animals have been conducted, finally enabling scientists to consider the abilities of nonhuman species when contemplating “what makes us human.” In vast fields of science, this opportunity

has been seized and has led to the upsurge of behavioral ecology as well as to the emergence of new fields, such as biological anthropology, and comparative and evolutionary psychology. The inclusion of animal models was decisive about reframing models of human evolution within modern evolutionary theory thinking of adaptation and fitness benefits (Jolly, 1999; Maynard Smith, 1982; Trivers, 1971; Wilson, 1975). However, researchers have to acknowledge that this is still an ongoing process and that although some research disciplines have welcomed such new information, others have been slow or inconsistent at including field data.

Moreover, a new debate concerning the shortcomings and benefits of observational data has led to a resurgence of interest in captive studies as the main source for understanding cognitive capacities in animals. On the one side, some have argued that field data are just anecdotes and are therefore of a limited scientific value, as only experiments allow to control for the influence of possible different confounding factors (Bernstein, 1988; Hauser, 2000; Heyes, 1998; Povinelli, 1996, 2000; Tomasello & Call, 1997), whereas others argued that because of the logistic difficulties of fieldwork, key observations needed to explain observed patterns might always be missed (de Waal, 1982). On the other side of the debate, most argue that animals have evolved behavioral and cognitive traits, over hundreds of generations, needed to survive and thrive, and that animals should be studied under natural conditions if one wants to understand the full capacities of those animals (Boesch, 1993; Byrne, 1995; Cheney & Seyfarth, 1990; McGrew, 1992). Furthermore, captive living conditions are impoverished compared with natural ones, and therefore the development of abilities during ontogeny might be negatively affected (Boesch, 1993; Whiten, 2000). The debate on the relative importance of field observations versus controlled captive experiments, to my mind, find its roots in a striking disagreement on the

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Correspondence concerning this article should be addressed to Christophe Boesch, Max Planck Institute of Evolutionary Anthropology, Deutscher Platz 6, 04 103, Leipzig, Germany. E-mail: boesch@eva.mpg.de

theoretical approaches to the development of behavioral and cognitive capacities in individuals that needs to be clearly spelled out if researchers want to bring some clarity in this debate. Two key questions follow: Are differences in cognitive capacities observed between populations within a species? Do differences in the living conditions experienced during ontogeny affect the development of cognitive abilities?

Here, I first formulate the two different theoretical approaches that underlie the different positions that have been taken to address these questions and show how divergent the predictions of these approaches are. Next, I review some of the available data about cognitive differences between populations within both humans and chimpanzees (*Pan troglodytes*) to test the support for the different predictions, and finally I make some propositions as to how the understanding of species differences in the cognitive domain may be improved.

## Two Different Theoretical Approaches

### *Developmentalist Approach*

Modern evolutionary biology has shown that individuals inherit a genotype from their ancestors that interacts with the environment throughout the life of the individual to produce a full grown individual (e.g., Dawkins, 1986; Ridley, 1996; Stearns & Hoekstra, 2000). This genotype is already the product of the selection process faced by many generations and reflects the interactions with past environmental conditions. This approach postulates a constant interaction of the genetic make-up with the environmental conditions that may result in quite a range of outcomes (e.g., Cole, 2006; Geary, 2005; Laland & Janik, 2006; West-Eberhard, 2003; Williams, 1966; Wilson, 1975). So, each individual's abilities result from an interaction between history and experience.

Developmental biologists have amply demonstrated the importance of such interactions on morphological and behavioral traits in many species (e.g., Atkinson & Thorndyke, 2001; Wagner, Chiu, & Laubichler, 2000; West-Eberhard, 2003). The most dramatic cases include examples of fruit flies that are genetically identical but differ in many life history traits—such as age of first reproduction, number of eggs produced, and flying behavior—as a result of experiencing different living conditions during development (Stearns, 1992; Stearns & Hoekstra, 2000). This has been labeled *developmental reaction norms* and has been shown to be a general phenomenon. A predominant interest in the field of behavioral ecology is observing and explaining the variability of the social organization, foraging behavior and reproductive strategies of numerous species observed under varying ecological conditions (Alcock, 1989; Krebs & Davies, 1993; Wilson, 1975). It has become clear that the degree of diversity observed within species varies considerably and that such variation increases with learning abilities. Behavioral flexibility, measured by foraging innovation, social learning, and tool use, has been shown to increase, both in birds and in primates, with brain size (Lefebvre, Nicolakakis, & Boire, 2002; Lefebvre, Whittle, Lascaris, & Finkelstein, 1997; Reader & Laland, 2002).

So the question is whether such intraspecific variability also exists in cognitive domains. The theory of natural selection predicts that individuals will adapt to different environmental conditions to survive and be able to reproduce. Different precise pre-

dictions can be formulated: First, the more diverse the environmental conditions faced by an animal species, the more variation will be expected in the cognitive domain between populations of that species. Altitude and latitude affect climatic parameters that will determine the amount, type, and distribution of food sources, which in turn influence individual foraging strategies that require cognitive abilities in terms of orientation, mapping, causality understanding, and predicting. Foraging strategies will, in turn, affect the social structure, social group size, and social interactions that are the foundation of all social cognition abilities. Therefore, researchers predict that species with a larger distribution on the planet will present more variability in behavioral traits and cognitive abilities. Humans, with a much wider distribution on Earth than chimpanzees, are predicted to show more within-species variation in cognitive abilities than chimpanzees.

Second, different cognitive abilities are predicted to develop in a flexible way depending on the conditions experienced during ontogeny, and this will be more apparent in large brained species that have been shown to possess more learning abilities (Lefebvre et al., 2002; Reader & Laland, 2002). This will provide individuals with a flexible response allowing them to survive under more diverse conditions. A third prediction is that variation in cognitive abilities is expected to increase with greater niche differentiation within social groups. High within-group competition will result in certain classes of individuals (e.g., subadult, female, or low-ranking individuals) facing different environmental conditions than other classes, and this will lead to the development of different cognitive abilities. For example, low-ranking peripheral females in hamadryas baboon groups have been shown to explore and find more hidden food than high-ranking females (Sigg, 1980). Classic examples of this in noncognitive domains are (a) that low-ranking female baboons suppress reproduction totally during low food availability years, whereas high-ranking ones continue to reproduce normally (Altmann, 1980) or (b) that high-ranking female red deer produce more sons than do low-ranking females (Clutton-Brock, Albon, & Guinness, 1984).

In summary, under a developmentalist approach, cognitive development is predicted to be influenced by living conditions, and important intraspecific variation between populations is expected as a result of varied living conditions.

### *Deterministic Approach*

René Descartes postulated a fundamental difference between humans and animals, whereby he described humans as thinking animals but all other animals as machines following a prefixed program (Descartes, 1964–1973, in Bowler, 1989, p. 57). In other words, humans are born resembling a white sheet upon which everything can be written, whereas animals are genetically rigidly fixed. Under this approach, humans are proposed to be only influenced by experience, and animals only by history. Such a classic view has been held in social sciences and has been only challenged by the emergence of modern evolution theory. Its influence can be strongly seen in some circles of cultural and social anthropology (Barnard, 2000; Kuper, 1999).

Most striking is its prevalence in the field of psychology. This deterministic approach predicts that individuals' cognitive abilities are not influenced by experiences during development and that individuals develop full-fledged species-specific cognitive abilities

under a whole array of different environmental conditions. The main manifestation of this approach in psychology has been the general consensus that animal captive studies are fully representative of the cognitive abilities of the species as a whole. Throughout the recent literature, data collected with captive animals are presented as representing species-typical traits, without much discussions of the possible effect of experience on the cognitive abilities (e.g., Call, Carpenter, & Tomasello, 2005; Call & Tomasello, 1996; Galef, 1988, 1990; Heyes, 1993, 1994, 1998; Povinelli, 1994, 1996, 1999, 2000; Povinelli & Vonk, 2003; Premack & Premack, 1983; Tomasello, 1996, 1998, 1999; Tomasello, Carpenter, Call, Behne, & Moll, 2005; Tomasello, Kruger, & Ratner, 1993). This is especially puzzling as earlier workers assembled conclusive data demonstrating the negative impacts of captive conditions on the development of different cognitive abilities in primates (Davenport, 1979; Gallup, McClure, Hill, & Bundy, 1971; Harlow & Harlow, 1962, 1965; Harlow, Harlow, & Suomi, 1971; Hinde, 1971; Mason, 1965, 1978; Menzel, Davenport, & Rogers, 1961, 1970; Rogers & Davenport, 1969). Only few psychologists have kept to these pioneers in considering the possible impact of captive conditions and tried to address them while preserving the advantage of experiments that allow controlling for the influence of confounding variables (Byrne, 1995; de Waal, 2001; B. T. Gardner & Gardner, 1989; R. Gardner, 2005; Whiten, 2000). For example, one innovative Japanese group has pioneered the establishment of long-term triadic relationships between a mother chimpanzee, her infant, and a human tester followed by subsequent introduction of a unique face-to-face testing procedure (Imura, Tomonaga, & Yagi, 2006; Matsuzawa, 2006; Murai, 2006).

Regarding experimental psychology studies on humans, a strict deterministic approach seems, paradoxically, to have been developing for human studies, which is quite in opposition with what Descartes originally proposed. Indeed, researchers have collected a majority of experimental psychology data using White middle-upper class Westerners, and, despite the fact that this represents only a small minority of the societies present in humans, has generally been considered as representative for all humans, without preliminary testing of whether this generous assumption was true (see, e.g., Meltzoff, 1996; Piaget, 1935, 1945; Piaget & Inhelder, 1947; Tomasello, 1999; Wellman, Cross, & Watson, 2001). This approach seems surprising considering that historically, humans have been proposed to be so much more flexible than animals, and I hope that by making clear the assumption underlining the deterministic approach as applied to humans, some debates about it will emerge. The prediction of the deterministic view that individual experience does not count in human cognition needs to be tested.

Within the field of psychology, it is mainly cultural psychologists that have challenged this occidental-biased approach to human cognition (Berry, Poortinga, Segall, & Dasen, 2002; Dasen, Inhelder, Lavallée, & Reitschitzki, 1978; Dasen & Mishra, 2000; Haun, Rapold, Call, Janzen, & Levinson, 2006; Majid, Bowerman, Kita, Haun, & Levinson, 2004; Murray, 1999; Segall, Dasen, Berry, & Poortinga, 1999), but their contributions still need to be considered seriously by the experimental psychologists. At the same time, social psychologists have also invested a lot of time to demonstrate how socioecological conditions affect the development of cognitive capacities in humans (e.g., Carpendale & Lewis,

2004; Correa-Chavez & Rogoff, 2005; Holmes, Black, & Miller, 1996; Rogoff, 1990), and their contributions are important to balance the predominant importance given to data coming from White middle-upper class Westerners. On the other side, evolutionary thinking has been taken to an extreme by some in the field of evolutionary psychology, who are championing a strict deterministic approach to human cognition suggesting that history is determinant and experience counts only as a trigger leading to the full expression of particular genetically fixed cognitive modules (Evans, 2003; Sperber & Hirschfeld, 2004; Tooby & Cosmides, 1988).

The predictions about the respective roles of history and experience emerging from the developmentalist and deterministic approaches are quite different, making it possible to consider whether the data support either approach. More specific, if within-species variation in cognitive abilities is present in humans, then researchers need to reevaluate their conclusions about human cognitive abilities and redirect research efforts toward studying cognitive abilities in humans living under different cultural and environmental conditions. Furthermore, if this is also true for other animals, then most results in comparative psychology will need reconsideration, and much more care should be taken in making comparisons between species in the cognitive domain.

### Do Population Differences Exist in Cognitive Domains in Humans?

As cross-cultural psychology is still in its infancy, only a limited number of human societies have been studied, and researchers are still far from being able to document the whole of human cognitive variability. Nevertheless, the data available in some cognitive domains will allow researchers to test the different predictions about population differences in cognition. I focus upon data for two specific domains in which the largest set of comparative data is available, the notion of space and the understanding of others, often also called theory of mind.

#### *Notion of Space in Humans*

Two ways to address the notion of space have been identified; the first, following Jean Piaget, has been to look at the emergence of a topographic or a Euclidean notion of space during an individual's development (Piaget & Inhelder, 1947) (see Table 1). In White middle class Westerners (WMCs), a topographic space, based mainly on landmarks that are related to one another, emerges first by some 5 years of age and is later replaced by a more elaborate Euclidean space, in which coordinates are used to relate landmarks allowing to use shortcuts and measure distances between objects by the age of 10 years. In cross-cultural studies, a similar sequence of appearance has been confirmed in some cultures, although the age of emergence might be quite different (Segall et al., 1999). Hunter-gatherers, like the Inuit or the Aborigines, seem to acquire a Euclidean space systematically and quite early, whereas traditional farmers, like the Ebríé, are much slower in the acquisition of a full notion of space, and a large proportion of individuals do not seem to acquire a Euclidean notion at all (Dasen, 1982; Segall et al., 1999). It is interesting that sex differences have also been found in such a domain, with

Table 1  
*Comparisons of Some Spatial Notions in Use in Different Human Societies*

Cultural group	Performance	Reference
WMC	Topographic + Euclidean	Piaget & Inhelder, 1947
Inuit (Greenland)	Topographic + Euclidean	Dasen, 1982
Aborigines (Australia)	Topographic + Euclidean	Dasen, 1982
Ebrié (Côte d'Ivoire)	Topographic only	Dasen, 1982
WMC	Relative before absolute	Piaget & Inhelder, 1947
Vranisi (India)	Relative and absolute	Mishra et al., 2003
Tzeltal (Mexico)	Absolute before relative	Brown & Levinson, 2000
Tzotzil (Mexico)	Absolute before relative	De León, 1994
Bali (Indonesia)	Absolute before relative	Wassmann & Dasen, 1998
Roopchandpur (India)	Absolute before relative	Mishra et al., 2003
Bhimeshwar (Nepal)	Absolute before relative	Mishra et al., 2003
Hailom (Namibia)	Absolute before relative	Haun, Rapold, et al., 2006
Guugu Yimithirr (Australia)	Absolute only	Majid et al., 2004

*Note.* WMC = White middle class Westerner.

women having less spatial but more numerical abilities than men (Dasen, 1982).

Another way to look at the notion of space is to focus on the way individuals place objects in space (Levinson, Kita, Haun, & Rasch, 2002; Majid et al., 2004), as objects can be placed in relation to others (e.g., to the left or right), producing a so-called "relative" notion of space, or objects can be placed in absolute terms (e.g., in the north), following an "absolute" notion of space. In the WMCs, a relative notion emerges first, and even if an absolute one emerges later, the former will remain the main one used (Levinson et al., 2002). This sequence of emergence has been confirmed in some cultures, whereas in others a reversal has been observed whereby the absolute notion emerges first and remains the one used in most situations (see Table 1). In one case, the absolute is the only one present. Contrary to what has been observed in Westerners, studies on two groups of Mayans, the Tzotzil and the Tzeltal, have revealed that they mainly use an absolute concept of space that they acquire remarkably early in life (Brown & Levinson, 2000; De León, 1994). The Tzeltal living in southern Mexico have a distinct linguistic repertoire for talking about spatial relations that is based on an absolute notion of space in which, for example, objects are placed up or down hill rather than left or right. Mayan children develop an absolute notion of space before a relative one, in contrast to what is observed in the occidental world. Balinese spatial orientation is even more absolute than that observed in the Maya, as Balinese space is directed toward the highest mountain of the island, Mont Agung, culminating at 1,800 m at the center of the island (Wassmann & Dasen, 1998). However, absolute directions point toward different cardinal directions in different villages, as each village is located at a distinct point around the mountain on this circular island's seashore. Furthermore, villages that have been established by migrants use their original village as the point of origin for determining the direction of the mountain. Such an extreme absolute notion of space forces men of different villages to agree beforehand on the bearing of each direction when playing a game based on orientation notions. Here, as in the Mayan case, it seems that the development of spatial knowledge is the converse of the occidental scenario.

### *Understanding of Others in Humans*

The ability to understand others as independent agents with their own knowledge and beliefs (i.e., theory of mind) has become a contentious topic of research because it intersects with the quest to understand differences between humans and chimpanzees. Some suggest it exists in chimpanzees (Premack & Woodruff, 1978), whereas many others propose it as a hallmark of humanity (Astington & Baird, 2004; Carruthers & Smith, 1996; Gopnik & Meltzoff, 1994; Hala & Chandler, 1996; Leslie, Friedman, & German, 2004; Meltzoff, 1995; Povinelli, 1996; Povinelli & Vonk, 2003; Tomasello, 1999; Tomasello et al., 2005; Tomasello et al., 1993; Wellman et al., 2001; Wimmer, Hogrefe, & Perner, 1988). I focus for comparison purposes on only one theory of mind test, the false-belief test, as it has by far been used the most frequently (see Table 2). The false-belief test requires the subject to predict where a third person will predict an object is hidden when that object location has been changed while only the subject was present. Typically, the majority of WMCs pass this test by the age of 4 years (Wellman et al., 2001). As can be seen from Table 2, similar development paths have been confirmed in some other populations in which children attend city schools. In other human populations, the time of successful understanding of the false-belief test can be markedly delayed to the point of not being observed in older children. More studies will be needed to know whether those noted as "absent" in Table 2 would remain so after older individuals were tested.

The frequent use of the false belief test allows researchers to test whether different childhood environments met by individuals within a same population affect the development of this cognitive ability (see Table 3). For example, within the United States, a study of people with low income, composed primarily of African American families, revealed that despite an improvement with age in false-belief tasks, they generally fell short of the level of performance reported from White middle class individuals; 37% passed the test by age 4 versus 61% in WMC samples, and 57% of the 5-year-olds were successful compared with 89% in the WMC samples (Holmes et al., 1996). Similar studies conducted with low income families, comprising mainly Caucasian subjects, in Oregon

Table 2  
*Comparison of the Ages at Which Individuals From Different Cultures Develop an Understanding of Others, on the Basis of Results of the False-Belief Test*

Cultural group	Performance	Reference
WMC	Present by 4 years	Wellman & Watson, 2001
Baka (Cameroon)	Present by 4 years	Avis & Harris, 1991
City school (Peru)	Present by 5 years	Callaghan et al., 2005
City school (India)	Present by 5 years	Callaghan et al., 2005
City school (Thailand)	Present by 5 years	Callaghan et al., 2005
Tolai (Papua New Guinea)	Present by 7 years	Vinden, 1999
Yukatek (Mexico)	Present by 7 years	Knight et al., 2004
Mofu (Cameroon)	Present by 9 years	Vinden, 1999
Village school (Samoa)	Absent at 5 years	Callaghan et al., 2005
Junin Quechua (Peru)	Absent at 5 years	Vinden, 1996
Tainae (Papua New Guinea)	Absent at 14 years	Vinden, 1999

*Note.* Presented are the ages at which the majority of individuals have been observed to succeed in the test. For the cases in which the individuals did not succeed, the oldest ages tested are listed. WMC = White middle class Westerner.

(Pears & Moses, 2003) and in London (Cutting & Dunn, 1999) have confirmed these results.

To further stress the importance of the environment experienced during childhood, Perner, Ruffman, and Leekam (1994) showed that besides family income, family composition revealed itself as well to be a major influence on false-belief test performance, as the number of siblings a child has positively affects the emergence of the understanding of others. After careful analysis, it was shown that it is the presence of older siblings, and not younger ones, that has this decisive effect (Ruffman, Perner, Naito, Parkin, & Clements, 1998). The more older siblings that are present, the earlier an understanding of others emerges, so that 4-year-old children with two older siblings are 2.4 times more accurate than those with younger or no siblings (see Table 3). Additionally, the quality of interactions within the family was also shown to accelerate the emergence of this ability, with mental stimulations by mothers and friendly relationships between family members having positive effects (Howe, Petrakos, & Rinaldi, 1998; Howe, Rinaldi, Jennings, & Petrakos, 2002; Slomkowski & Dunn, 1996).

This review of some experimental data on two cognitive abilities reveals that important differences between human populations emerge as a function of the living conditions faced during early

life. This strongly contradicts the deterministic approach but is in line with the predictions of the developmentalist one.

Similar conclusions have also been reached concerning other cognitive domains. For example, naïve or folk biology has been proposed to be implicitly universal, as all people around the world need to be able to understand and predict the general properties of the objects around them. In an attempt to document this, researchers compared standard U.S. undergraduates (equivalent to the WMC group) with Itza Maya elders from Guatemala, and U.S. Ph.D. holders in botany, middle class children near U.S. universities, and Yutatek Mayans in rural Mexico (Atran, Medin, & Ross, 2005; Medin & Atran, 2004; Ross, Medin, Coley, & Atran, 2002). Most of these groups have the tendency to categorize objects and use them to think about biology, but their ways of categorizing animals and plants are strongly affected by experience. U.S. children in contact with nature possess more similarities with Maya elders without any formal education than with U.S. undergraduates. It is interesting that the researchers found that on most of the tasks, the U.S. undergraduate group failed to match the results of the other human groups. The authors accordingly suggested that U.S. undergraduates are atypical and that contemporary people in small-scale societies that continue to live intimately with

Table 3  
*Comparison of the Effect of Socioeconomic Conditions on the Emergence of an Understanding of Others in Humans*

Human group	Factor	Influence	Reference
Head Start	Low income	37% later	Holmes et al., 1996
London	Low income	20% later	Cutting & Dunn, 1999
WMC	No. of siblings	Positive effect	Perner et al., 1994
WMC	No. older siblings	2.4 times earlier	Ruffman et al., 1998
WMC	Social status	Negative effect	Rutherford, 2004
WMC	Dominance	Negative effect	Thomas et al., 1972
WMC	Maternal style	Positive effect	Pears & Moses, 2003
WMC	Relation quality	Positive effect	Howe et al., 2002

*Note.* Under "Influence" are presented the delay or acceleration in the performance compared with the WMC performance (positive effect/negative effect = performance accelerates/delays as the factor increases). WMC = White middle class Westerner.

nature are more representative of humanity (Medin & Atran, 2004). Similarly, large differences in causal reasoning between East Asians and Westerners (represented by Americans, Canadians, and Europeans) have been documented (Choi, Nisbett, & Norenzayan, 1999; Nisbett, Peng, Choi, & Norenzayan, 2001; Norenzayan & Nisbett, 2000; Norenzayan, Smith, Kim, & Nisbett, 2002). To summarize, East Asians use a holistic approach that takes into account the situations and constraints of an object and assigning causality to it, making relatively little use of categories or formal thinking, whereas Westerners are more analytical, primarily paying attention to the object and the categories to which it belongs while using rules to understand its behavior (Nisbett et al., 2001). The result is that East Asians—including Korean, Japanese, and Chinese people—judge causality in quite different ways and disagree on many judgments with U.S. White middle class subjects. This large difference has been proposed to be already apparent in the way that classical philosophy and science has been done in the past (Nisbett et al., 2001).

Also noteworthy is that counting abilities seem to be affected by the socioeconomic environment. For example, the Oksapmin of Papua New Guinea are famous for counting by employing names of body parts (e.g., 1 is the thumb of the right hand, 12 is the right ear, or 23 is the thumb of the left hand; Saxe, 1981, 1982; Saxe & Moylan, 1982). Such a system works only for a limited number of items, and addition problems—including more than 27 objects—are unsolvable. Oksapmin traditionally do not count with objects they do not see, and no representational solution exists in the absence of objects. This counting system progressively gave way to numerical conventions similar to the Western ones starting in 1961 when missionaries and government officers introduced the first money and trade shops (Saxe & Esmonde, 2004, 2005). Similarly, Bantu language in Africa contains only five words for numbers, and the Zulu language in South Africa has numbers referring only to finger gestures (Zaslavsky, 1973), whereas Mundurucu and the Pirahã languages in the Amazonia that lack words for numbers beyond five, fail in exact arithmetic with numbers larger than five (Gordon, 2004; Pica, Lemer, Izard, & Dehaene, 2004). In Africa as well, the introduction of coins and shops has led to a shift of counting by using more numerals (Saxe & Esmonde, 2005; Zaslavsky, 1973). A recent study comparing native Chinese and English speakers dramatically illustrates how differences in experience faced during the ontogeny can lead to remarkable alteration in brain function during mathematical problem solving (Cantlon & Brannon, 2007; Tang et al., 2006).

To conclude, despite the fact that the data are preliminary and represent only a small subset of the human population diversity, the trend is clear in showing that large differences in cognitive domains exist between human populations and that the environmental conditions they face affect their performances. Therefore, the assumption that WMC subjects are representative of all humans is strongly contradicted. This represents a challenge for the understanding of human cognition, as researchers need to take in account the breadth of diversity of performance present in humans rather than restrict themselves to the performance of a single population. In addition, it is important to understand which factors of the environment affect the development of specific cognitive abilities (as can be seen in Table 3).

Diversity in human cognitive performance represents a great challenge to a deterministic approach in comparative psychology

and may have major consequences for the way researchers try to answer the question of “what makes us human.” The inclusion of all possible human cognitive development pathways will question most present claims about human cognitive uniqueness. For example, the ability to understand others emerges in WMC humans by the age of 4 years. Relying on that age, researchers have done all comparisons on this ability with chimpanzees or other apes using young subadult individuals. If, however, the emergence of this ability can happen in normal humans much later, as documented in Table 2, it follows that researchers also need to allow for possible later maturation of this ability in apes before drawing any conclusions about species differences. Similarly, family size and composition plays a significant role on the time of emergence of this ability in humans (see Table 3). Given the very close proximity of apes to humans, it is parsimonious to admit that such factors likely also play some role in apes. So, comparisons with apes should only include individuals that have grown up in complete families with older siblings, and data collected with individuals that have grown up under socially deprived captive conditions should be discarded. A similar variability has been observed for the notion of space in which an absolute notion seems to be mastered by children between 4 and 7 years, whereas a relative notion is mastered only at an age of about 11 years (Haun, Rapold, et al., 2006). Cross-species comparisons need to take into account such possible large time delays in maturation in a notion of space.

#### Do Population Differences in Cognitive Domains Exist in Chimpanzees?

If cross-cultural studies in humans are in their infancy, the study of differences between populations in chimpanzees is even less developed. Only 11 populations have been studied with enough detail to permit a preliminary listing of potential cultural differences in that species (Whiten et al., 1999). In addition, the general acceptance of captive studies as representative for the ability of an animal species has strongly discouraged cognitive studies with wild populations.

From a deterministic point of view this is not a problem, as population differences in cognitive abilities are expected to be negligible, and captive populations of chimpanzees would be considered as the most appropriate study individuals. This approach considers chimpanzee cognitive development as not affected by experience and context and assumes that they “act merely as slavish vehicles of the genes” (Evans, 2003, p. 458). From a developmentalist standpoint, in contrary, the development of cognitive abilities is predicted to be dependent upon the conditions faced during the upbringing. Thus, captive chimpanzees would possess cognitive abilities reflecting their captive living conditions, and these abilities are predicted to be quite different from those required to survive and be able to reproduce in the wild. This does not challenge the fact that captive studies in chimpanzees have been instrumental in revealing some major facets of their cognition, such as self-recognition (Gallup, 1970), symbolic abilities (B. T. Gardner & Gardner, 1989; Savage-Rumbaugh, Rumbaugh, & Boysen, 1980), theory of mind (Premack & Woodruff, 1978), and some aspects of their social strategies (de Waal, 1982). Indeed, such captive studies can be very important for the understanding of the evolution of cognitive abilities.

Thus, the central question is whether the conditions of a chimpanzee's upbringing affect its cognitive abilities. Direct evidence is fairly limited and mainly restricted to studies comparing captive chimpanzees living in socially and environmentally deprived situations with those experiencing enriched social and environmental conditions (with many objects and daily interactions with conspecifics or human caretakers). Such social and physical enrichment remarkably improves the primate's performance on different problem-solving and social-learning tasks (Davenport, 1979; Harlow et al., 1971; Mason, 1978; Menzel et al., 1961; Rogers & Davenport, 1969; Savage-Rumbaugh, Rumbaugh, & Boysen, 1978). In a precise study comparing lab-reared chimpanzees with cross-fostered and wild ones, B. T. Gardner and Gardner (1989) showed that the rearing environment differences between the three groups led to large differences in the time of emergence in many positional and locomotory behaviors. It is interesting that the enriched captive conditions faced by cross-fostered chimpanzees were very favorable, and their development was in many ways similar to the wild ones.

Studies on self-recognition have classically used the mirror test to study this capacity in different species (Gallup, 1970) and have been done with different primate species. Results indicate that only a few species pass the test successfully, leading to the suggestion that only humans, chimpanzees, gorillas, and some orangutans have a notion of self (Byrne, 1995; Eddy, Gallup, & Povinelli, 1996; Gallup et al., 1971; Hauser, 2000; but see recent positive result in elephants, Plotnik, de Waal, & Reiss, 2006, and dolphins, Reiss & Marino, 2001). However, the performances of the chimpanzees were mixed, as some succeeded, whereas others did not. A careful analysis of the evidence suggested that early experience of the individual explains these results, with individuals living in isolation failing the tests, whereas those having a richer social environment succeeding (de Veer & Van de Bos, 1999; Gallup et al., 1971; Van de Bos, 1999). Thus, empirical evidence clearly shows an effect of ontogenetic experience on cognitive abilities in chimpanzees.

More abundant evidence points clearly toward a strong effect of living conditions on the cognitive performance of the chimpanzees. The single most important result of the last two decades of study of wild chimpanzees was the description of large intraspecific behavioral diversity, including all aspects of their behavior, ranging from social group size, group composition, and social interactions to sexual behavior, tool uses, hunting strategies, feeding techniques, and cultural traits (Boesch & Boesch 1989, 1990; Boesch & Boesch-Achermann, 2000; Boesch, Hohmann, & Marchant, 2002; McGrew, Nishida, & Marchant, 1996; Mitani, Watts, & Muller, 2002; Whiten et al., 1999, 2001; Wrangham, McGrew, de Waal, & Heltne, 1994). Given that large parts of the chimpanzee range are totally unknown to science, researchers must assume that this behavioral diversity will only increase as more new populations are studied. For example, new types of tool uses have been described in the Goulougo Triangle chimpanzees of northern Congo (Sanz, Morgan, & Gulick, 2004); in Cameroon (Morgan & Abwe, 2006), cave use along with spear use in hunting have been described for the first time in this species; in Senegal (Pruetz, 2001; Pruetz & Bertolani, 2007), well-digging in Semliki chimpanzees from Uganda (Hunt & McGrew, 2002) and feeding on underground tubers in Tongo chimpanzees from the Democratic Republic of Congo (Lanjouw, 2002) have been described.

In addition, there is a large and growing body of evidence showing that in other species the conditions of upbringing directly affect performance on psychological tests. The famous dog, Rico, that has been lovingly trained by her owner for years to learn hundreds of toys by name out-competed the performance of other dogs on some learning tasks and exhibited some learning abilities previously thought to be restricted to humans (Kaminski, Call, & Fischer, 2004). Similar effects has been observed for parrots and captive chimpanzees that were reared in rich environments featuring constant contact with human caretakers and daily enrichment and stimulation in the form of artificial language training lessons (de Waal, 2001; Pepperberg, 1987; Savage-Rumbaugh et al., 1980).

In conclusion, all evidence suggests that experience is very important and seems to affect cognitive development in chimpanzees. This is clearly in agreement with the predictions of the developmentalist approach and conflicts with the deterministic approach. In other words, many of the conclusions reached by comparative psychology experiments are based on unreliable assumptions. I am suggesting that researchers need to take into account the upbringing conditions of the subjects they are testing if they are going to understand cognitive differences between species.

#### Designing Ways to Compare Species: The Experiment Paradox

Experimental studies exploring interspecific differences in behavior need to rely on carefully designed procedures for the comparison to be valid. Experiments should be favored when different, alterable factors may lead to the observed behavior. In theory, experiments work by manipulating the variables that are of interest while keeping constant those that are not (Campbell & Stanley, 1963, 1966; Spector, 1981). To accomplish such an ideal, some have tried to present similar conditions to both human and chimpanzee subjects, for example, both were tested in the same cages (Wolfe & Wolfe, 1939). In practice, however, the vast majority of experimental procedures used in comparative cognitive sciences violate this central experimental paradigm. In the comparative cognitive studies including human subjects, many key differences are systematically introduced into the experiment procedures:

1. Human subjects are selected from free-ranging individuals living in natural social groups, whereas ape subjects are selected from captive individuals living in deprived social groups;
2. Human subjects are tested with conspecifics, whereas ape subjects are tested with members of another species (normally humans);
3. Humans subjects are tested in the same room as the experimenters, whereas ape subjects are separated by physical barriers from the experimenters;
4. Infant human subjects are in close proximity to one of their parents during testing, whereas infant ape subjects are separated from their biological mothers during testing;

Table 4

*Presence of Biases Introduced in Experimental Procedures in Recently Published Comparative Work, Including Humans and Apes*

Species compared	Bias 1 captive	Bias 2 conspecific	Bias 3 barrier	Bias 4 parent	Bias 5 artificial	Outcome <sup>a</sup>	Reference
H-C-G-O	x	x	x		x	H = C	Barth & Call, 2006
H-C	x					H = C	Horner et al., 2006
H-C-G-O	x	x	x	x	x	H > C	Haun, Call, et al., 2006
H-C	x	x	x	x	x	H > C	Collier-Baker & Suddendorf, 2006
H-C-O	x	x	x	x	x	H > C	Poss & Rochat, 2003
H-C-O	x	x	x	x	x	H > C	Call, 2001
H-C	x		x		x	H ≠ C	Fagot & Tomonaga, 1999
H-C-O	x	x		x		H = C	Itakura & Tanaka, 1998
H-C-O	x	x	x	x?	x	H > C	Call & Tomasello, 1998
H-O	x	x	x			H = OO	Call & Tomasello, 1996
H-C	x	x	x/-	x/-		H > C	Whiten, 1996
H-O	x	x/-	x/-		x	H > O	Call & Tomasello, 1995
H-C	x	x		x	x	H > C	Warneken et al., 2006
H-C-G-O	x	x	x	x	x	H > C	Haun, Rapold, et al., 2006
H-C	x	x	x	x	x	H > C	Warneken & Tomasello, 2006
H-C-O	x	x	x		x	H > C	Call & Tomasello, 1999
H-C	x				x	H ≠ C	Call et al., 2005
H-C	x/-	x				H < C	Horner & Whiten, 2005
H-C	x		x		x	H ≠ C	Fagot & Tomonaga, 2001
H-C	x	x	x	x?	x	H > C	Call, 2001
H-C	x	x			x	H ≠ C	Tomonaga, 1998
H-C-B	x	x	x	x	x	H > C	Herrmann & Tomasello, 2006
H-C	x	x				H = C	Murai, 2006
Total	23	19	17	12	17		
%	100	82	74	52	74		

*Note.* For further explanation on the five experimental biases, refer to the text. H = human; C = chimpanzee; G = gorilla; O = orangutan; B = bonobo; x = bias being present; x? = bias most likely present but not mentioned in the method; x/- = bias present for only some of the group tested.

<sup>a</sup> Outcomes are presented according to the judgments made by the authors of the studies; H = C when both species performed equally; H > C when humans were judged to perform qualitatively in a more elaborate way than chimpanzees; H < C when chimpanzees were judged to perform qualitatively in a more elaborate way than humans; H ≠ C when both species performed differently, and the authors did not judge any one way as better.

- Human subjects are tested about conspecific tasks with conspecific materials, whereas ape subjects are tested about human tasks with human materials.

The introduction of such systematic biases in the experimental procedures is very questionable, as it might directly affect the outcome of the experiments (see de Waal, 2001). In a review of the last 10 years in 12 top scientific journals and magazines,<sup>1</sup> I found 23 publications directly comparing human with chimpanzee performance on cognitive tasks (see Table 4). All of them compared captive chimpanzees with free living humans that were in all cases young children living in their natural families and that came to the research institutions only for the experiments. The vast majority used human experimenters/demonstrators with the chimpanzees and physical barriers to isolate the chimpanzees from the human experimenters. Significantly more studies that used physical barriers for chimpanzees and not for humans concluded that humans were superior to chimpanzees than those studies avoiding the use of physical barriers (barrier: 13 of 16 studies; no barrier: 1 of 7 studies; Fisher exact test:  $p = .0049$ ). Similarly, significantly more studies that allowed the presence of one parent only for human children concluded that humans were superior to chimpanzees than studies that avoided the presence of parents during the testing (parent present: 11 of 12 studies; no parent: 3 of 11 studies; Fisher exact test:  $p = .0028$ ). Finally, all comparative studies that used physical barriers and allowed the presence of one parent for

children concluded that humans were superior ( $n = 10$ ), whereas none of the studies avoiding both did so ( $n = 5$ ; Fisher exact test:  $p = .0003$ ). It is interesting that in this data set the use of a human experimenter did not seem to have an influence on the conclusion that humans perform better than chimpanzees (Fisher exact test:  $p = .126$ ). Taken together, this review highlights the large impact some aspects of the testing procedures might have on the results in a species comparison test.

Striking examples of such biased procedures are seen when researchers compare—for the understanding of communicative signals—Westerner human subjects sharing the same room with the experimenters and one of their parents with subjects of one species isolated behind physical barriers from the experimenters (see pictures illustrating this in Bräuer, Kaminski, Riedel, Call, & Tomasello, 2006; Herrmann & Tomasello, 2006; Povinelli, 2000). This biased procedure alters some important features of the communicative signals presented: For example, a pointing gesture would be either directly aimed at one object (the same room condition) or indirectly through another object (the physical barrier condition) while at the same time affecting the distance separating

<sup>1</sup> The journals and magazines reviewed include the following: *Journal of Comparative Psychology*, *Animal Cognition*, *Journal of Experimental Psychology*, *Animal Behaviour*, *Science*, *Nature*, *Developmental Psychology*, *Current Biology*, *Cognition*, *Developmental Science*, *Developmental Psychology*, and *Behavioural Processes*.

the objects, which is known to influence species-specific perception in chimpanzees and humans (Fagot & Tomonaga, 2001).

Although I can fully understand why some of these biases are introduced, for example it might be very stressful to separate a baby from its mother, it remains that biased interspecific treatments introduce a systematic confounding variable into the experimental protocol. Because such bias could lead to important differences in the results between the two groups tested, it is puzzling that the effect of such differences has never been systematically studied. The introduction of Bias 4 (parent present) is even more problematic, as it allows for extensive uncontrolled “Clever Hans” effects—named after the horse whose apparent mathematical knowledge was derived from its ability to read unconscious clues provided by its owner/experimenter. By allowing for physical contact in experiments (children are often sitting on the lap of one of their parents, or they have direct visual contact with a parent), experimental procedures allow for many uncontrolled clues to be exchanged (see the following video sequence from Warneken & Tomasello, 2006, which perfectly exemplifies how uncontrolled Clever Hans effects influence human children when tested with one of their parents present: [www.sciencemag.org/content/vol311/issue5765/images/data/1301/DC1/11211448s3.mpg](http://www.sciencemag.org/content/vol311/issue5765/images/data/1301/DC1/11211448s3.mpg)). Only recently have some researchers started to address the effects of different methods used within one species on the performance of the subjects and have concurred in concluding that it yields different results (Barth, Reaux, & Povinelli, 2005; Miklósi & Soproni, 2006; Sousa, Okamoto, & Matsuzawa, 2003). Adding control trials to evaluate the effects of the different bias introduced in such experiments would easily allow quantifying them, but as far as I know this has never been done.

In addition, such systematic differences are perceived as bias even by those who use them, as they will be avoided whenever judged possible. For example, in cognitive experiments comparing dogs with other species, the captive and physical barrier biases were not imposed on the dogs (see pictures of experiment procedures in, e.g., Bräuer et al., 2006; Hare & Tomasello, 2004; Miklósi, Pongracz, Lakatos, Topal, & Csanyi, 2005), even when apes and dogs were directly compared (Bräuer et al., 2006). In the discussion about dogs, chimpanzees, and human cognitive abilities, the fact that only the chimpanzees were forced to experience the captive and physical barrier biases has never been considered.

The other major problem with such systematic biases is that experiments that were designed to answer one question might actually address a very different one. Bias 2 (human experimenter) confuses the issues of within- versus between-species cognitive knowledge. For example, Bias 2 does not allow investigation of the presence of a theory of mind in chimpanzees but only the ability of chimpanzees to attribute a theory of mind to humans (see also de Waal, 2001). These two questions have been systematically confused (Povinelli, 1994, 1996; Povinelli & Vonk, 2003; Premack & Woodruff, 1978; Tomasello, 1999; Tomasello et al., 2005), and only in a very few number of studies in which chimpanzees have been tested with other chimpanzees has the first question been addressed (Hare, Call, Agnetta, & Tomasello, 2000; Hare, Call, & Tomasello, 2001). As is the case in humans (Barrett, Richert, & Driesenga, 2001), chimpanzees do better when tested on their understanding of conspecifics than on their understanding of members of other species.

The use of experiments in comparative psychology faces a paradox. They are favored because such experiments are an effective and sometimes the only way to systematically control for the effects of a single factor, but at the same time, they are systematically biased by the introduction of asymmetrical treatment conditions potentially disfavoring one of the two species compared. My recommendation would be to compare what is comparable. To that end, researchers should discern and avoid bias in experimental designs or to the least evaluate the effect of such biases if they cannot be avoided.

At the same time, one gets the impression that researchers must choose between doing controlled experiments in captive settings or collecting uncontrolled anecdotes from observing wild animals (Bernstein, 1988; Tomasello & Call, 1997). However, such a dichotomy is a pure artifact of different schools of thought. Behavioral ecologists—since the pioneering works of the field’s founders, Niko Tinbergen and Konrad Lorenz—have been conducting experiments in the field with wild animals (Alcock, 1989; Krebs & Davies, 1997; Lorenz, 1981; Ridley, 1996; Tinbergen, 1951). For example, many aspects of reproductive strategies, partner choice, and feeding tactics have been elucidated thanks to cleverly designed experiments done in the field that included controls for alternative explanations. Therefore, I think it is time to move away from such an artificial dichotomy and to take on the challenge of doing experiments in the field in primate studies, as has been done successfully by a few pioneers (Cheney & Seyfarth, 1990).

## Discussion

To understand how humans are different from other species, researchers need comparison of cognitive abilities among humans and other species—particularly between humans and their close relatives the African great apes. However, the comparative approaches taken in most psychological studies are of questionable value for two major reasons: First, differences within species have not been taken into account, and second, experimental procedures have differed systematically between species. Thus, what has been presented as “comparisons between humans and chimpanzees” has really represented “comparisons between WMC humans and captive chimpanzees.” Any comparison between humans and chimpanzees requires an assessment of the breadth of variation in the emergence and presence of cognitive abilities within each species. Different environmental conditions or upbringing experiences affect the emergence and development of different cognitive abilities. Each one population in a given species may thus represent only one point within the spectrum of the cognitive variability present within that species. The social deprived environment and limited physical demands of some captive conditions are predicted to select for limited cognitive skills in those domains, as will the nature sterile lifestyle of Westerner city dwellers in the domain of folk biology.

This review shows that individuals need a phase during their up-bringing during which they face conditions that challenge them for any experienced-based ability to develop. Such an “ecological imprint” would select for the development of ability to solve such challenges. If, however, the situations are never or infrequently encountered, experienced-based cognitive abilities will remain absent or develop only partially. Some cultural psychologists have

proposed an eco-cultural model to explain differences in the cognitive development observed between some human cultures (Segall et al., 1999), and some social psychologists have proposed a similar idea to explain the development of some social cognitive traits (Carpendale & Lewis, 2004). I propose, however, to generalize this idea to all large brain animal species capable of learning for which social and ecological experiences in early life are going to be determinant for constructing their cognitive abilities. Such ecological imprints have been documented in humans, for example, (a) when the acquisition of theory of mind abilities is facilitated when more specific social stimulations are encountered early in life (Carpendale & Lewis, 2004; Cutting & Dunn, 2006; Peterson & Slaughter, 2003; Ruffman et al., 1998; Ruffman, Slade, & Crowe, 2002), (b) when coins and cash economy practice facilitates the acquisition of abstract and representational arithmetic (Saxe & Esmonde, 2004, 2005), or (c) when the traditional farming way of life selects for a topographic notion of space, whereas a hunter-gatherer one favors a Euclidean notion of space (Dasen, 1982). Ecological imprinting predicts that individuals growing in isolation or impoverished social environments will acquire less social skills than those living in large families within large social groups. Similarly, it expects that animals living in a cage will acquire less spatial knowledge than those ranging freely within a 15 km<sup>2</sup> home range of tropical rainforest. Therefore, cross-species comparisons should be restricted to individuals that have faced a similar ecological imprint.

Comparing individuals that have faced different ecological imprints will almost per definition lead to significant differences that, however, do not reflect species differences. The famous example of Kanzi, the baby bonobo, growing near his mother that was daily trained without success to use symbolic signs for years (whereas Kanzi spontaneously developed sophisticated skills that still set him apart from other apes), illustrates well how special imprinting situations dramatically stimulate the development of cognitive capacities (Savage-Rumbaugh, et al., 1980). Similar results were seen with Ai, the female chimpanzee that has been solving arithmetic problems for the last 25 years, whose infant watched her solve many tasks and later developed spontaneously exceptionally early and proficient skills at match-to-sample tasks (Sousa et al., 2003). Some have spoken of enculturated apes developing human-specific abilities (Call & Tomasello, 1996; Tomasello, 1999) without appreciating that upbringing experience is a natural process faced by all individuals that has a key influence on experienced-based cognitive development (see also de Waal, 2001).

Comparing cognitive abilities of different species under an evolutionary approach will allow realizing (a) that cognitive abilities might not be totally similar in all members of one species, (b) that cognitive abilities are affected by the living conditions, and (c) that researchers need to think in terms of variance in cognitive abilities. Favoring comparisons between individuals of different species that faced similar ecological imprinting experiences under similar sets of natural selection pressures will permit more meaningful comparisons. The variance of cognitive abilities is expected to be larger in humans, as they live in more diverse environmental conditions than any other primates, and this might well be a specificity of the human species. Until this is done, many of the conclusions of species differences in cognitive domains are artifacts based on unequal comparisons and do not reflect true species differences. Greater care in comparing species is required if re-

searchers ever want to answer the question of “what makes us human.”

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