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A critical review of the “enculturation hypothesis”: the effects of human rearing on great ape social cognition

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Abstract Numerous investigators have argued that early ontogenetic immersion in sociocultural environments facilitates cognitive developmental change in human-reared great apes more characteristic of *Homo sapiens* than of their own species. Such revamping of core, species-typical psychological systems might be manifest, according to this argument, in the emergence of mental representational competencies, a set of social cognitive skills theoretically consigned to humans alone. Human-reared great apes’ capacity to engage in “true imitation,” in which both the means and ends of demonstrated actions are reproduced with fairly high rates of fidelity, and laboratory great apes’ failure to do so, has frequently been interpreted as reflecting an emergent understanding of intentionality in the former. Although this epigenetic model of the effects of enculturation on social cognitive systems may be well-founded and theoretically justified in the biological literature, alternative models stressing behavioral as opposed to representational change have been largely overlooked. Here I review some of the controversy surrounding enculturation in great apes, and present an alternative nonmentalistic version of the enculturation hypothesis that can also account for enhanced imitative performance on object-oriented problem-solving tasks in human-reared animals.

Keywords Enculturation · Social cognition · Evolution · Developmental systems · Chimpanzees

Introduction

Whether chimpanzees routinely make inferences about intentions and desires, or appeal to higher-order cognitive

states such as beliefs and knowledge, remains a contentious issue (Heyes 1998; Hare 2001; Povinelli and Bering 2002; Suddendorf and Whiten 2001). These are not necessarily equivalent causal frameworks. Cognitive developmentalists have demonstrated in a number of experiments that an understanding of intentions occurs earlier in human infancy than does the more metarepresentational capacity used to reason about beliefs and knowledge, which is first seen in children’s reasoning around the fourth year of life and is usually referred to as a “theory of mind” (for a review, see Flavell 1999). Although intentionality and metarepresentation are separable and appear at different times in human ontogeny, they are usually envisioned as being part of the same cognitive system, a system devoted to processing the mental states of the self and others and that displays increasing complexity over the course of human development and, perhaps, throughout a relatively recent phylogeny as well (Suddendorf and Whiten 2001; Tomasello et al. 2003).

According to some researchers, it is therefore very possible that a closely related extant species could develop, given the right experiences, some “rudimentary level” of intentionality without it ever becoming the sophisticated metarepresentational stance of older children and adult humans (Tomasello et al. 2003), even if the system is normally absent in such species. In accounting for the greater levels of imitative behavior in human-reared over mother-reared captive chimpanzees, for example, Tomasello et al. (1993a, p. 1703) stated, “It is our contention that raising chimpanzees in a human-like cultural environment leads their ontogeny in a different direction than would be the case in their species-typical environment – a case of the same genotype leading to different phenotypes in different environments.” More specifically, the authors claim that “what is developing in chimpanzees as a result of their enculturation is not just imitative abilities, but rather more fundamental social-cognitive skills” (Tomasello et al. 1993a, p. 1702).

Tomasello, Call, and their colleagues have since championed this “enculturation hypothesis” in numerous articles and book chapters (Tomasello et al. 1993b, 1997;

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Call and Tomasello 1994, 1996; Carpenter et al. 1995; Tomasello 1996a, 1996b; Tomasello and Call 1997). The hypothesis has been most clearly stated in Call and Tomasello's (1996, p. 394) comprehensive review of both anecdotal reports and experimental findings of enhanced social cognitive abilities in human-raised great apes, particularly with regard to social learning. They write:

Our hypothesis is that being treated intentionally by others, i.e. being enculturated into a cognitive community, is an integral part of the ontogeny of certain sociocognitive abilities, especially the ability to understand behavior intentionally. It may be especially important to have such experiences early in development. This then leads to a number of specific ways in which apes behave with humans and conspecifics after they have come to understand behavior in this way, mostly involving access to the referential triangle in which the intentions of two participants are mutually understood.

According to Call and Tomasello (1996), what develops in these human-reared apes (and does not develop in chimpanzees living in the wild or reared by conspecifics in the laboratory) is a basic understanding of intentions – an understanding that other agents go about various tasks because they are attempting to attain some goal state. Although they speculate that such effects are facilitated by the “referential triangle” comprising joint attention episodes between the enculturated animals and their human caregivers that are focused on some common, third entity, the authors confess that the actual developmental mechanisms by which these purportedly species-atypical social cognitive abilities emerge in enculturated great apes remain unknown. Tomasello (1996a, p. 302) speculates that, “although we do not know for sure, it seems evident by comparing the different procedures used with different degrees of success with human-reared apes that the key element may be the learner's participation in routine cultural activities in which an adult human treats the ape intentionally by directing its attention, encouraging its behavior (including imitation), and the like.” As a consequence to this developmental process, he claims that, “[human-reared great apes] are coming to view others as intentional agents” (Tomasello (1996a, p. 290).

Debating the evolutionary antecedents of intentionality

Such a hypothesis, at least on its surface, seems to support the notion of basic evolutionary continuity, wherein contemporary structures found in closely related extant species are seen as variants or elaborations of a basic structure found in the common ancestor. This common ancestor may have been equipped with a broad enough range of reaction to potentiate novel aspects of the structure in different environmental contexts, aspects that became more specialized during subsequent speciation. In the case of humans and chimpanzees, molecular DNA analyses and other anthropological assays suggest that the two species last shared a common ancestor approximately 5–7 million

years ago (Parker and McKinney 1999; Pennisi 2002). Since that time, there have existed about a dozen species of humans, with the current representative (*Homo sapiens*) being the only remaining form and appearing in sub-Saharan Africa about 150,000 years ago (Johanson and Edgar 1996; Tattersall 1998). In contrast, chimpanzees (*Pan troglodytes*) appeared in their present form about 2 million years ago, at which time they diverged from bonobos (*Pan paniscus*) (Gagneux et al. 1999). Due to this relatively recent shared ancestry between humans and the genus *Pan*, many comparative scientists (e.g., de Waal 1982; Goodall 1986; Suddendorf and Whiten 2001; Fouts et al. 2002) believe that for any cognitive mechanism that is seemingly unique to humans, such as the ability to reason about mental states, something like an evolutionary precursor should occur in living chimpanzees, and perhaps even in orangutans, with whom we last shared a common ancestor about twelve to fifteen million years ago (Parker and McKinney 1999).

For example, in a recent review, Suddendorf and Whiten (2001, p. 629) note that, “parsimonious phylogenetic reconstruction suggests that great apes and humans share some sophisticated representational skills due to our common ancestry – even though a fully representational theory of mind may have evolved in our ancestors only after the split from the line that led to modern chimpanzees.”

Importantly, these authors claim that there is sufficient evidence that even laboratory-raised chimpanzees and those in the wild display the representational abilities for understanding intentions. Although this makes the issue of enculturation as it affects understanding intentions somewhat moot from their point of view, Suddendorf and Whiten nevertheless consent that, “enculturation does have the potential to modify the cognitive abilities of apes” (Suddendorf and Whiten 2001, p. 644). However, they express concerns about just how much modification occurs under such conditions. Namely,

[i]t is likely that...environmental extremes, such as living in isolation in a small cage or being home-reared in a stimulating human environment, have a drastic developmental impact. When differences between members of these two groups are found, it is not clear whether one should attribute differential performance to the positive effects of enculturation in one group or to the negative effects of an impoverished environment in the other. From this perspective, what human enculturation may be doing is mimicking the natural social environment of wild apes in important respects, allowing the individual to develop to its full capacity in a way it cannot when reared in meager captive conditions (Suddendorf and Whiten 2001, p. 644).

This position is similar to that held by Boesch (1993), who argues that chimpanzees develop their most sophisticated social cognitive skills in the wild (see also Parker and McKinney 1999). Unfortunately, this is largely an untestable proposition because it is not possible to subject wild apes to controlled experimentation and to compare their performance to that of laboratory animals. However,

stating that human enculturation “mimicks” the natural social environment of wild apes, even in “important respects,” may be misleading. There are many natural, normative behaviors emitted by human caregivers (e.g., attending to infants’ imperative demands, establishing joint attention, explicit teaching, engaging in pretend play, actively encouraging imitation) that do not appear to occur with any frequency among wild great apes, if at all (Tomasello and Call 1997; Bjorklund and Pellegrini 2002). In addition, few laboratory chimpanzees are now raised in social isolation, but are instead born into medium- to large-sized social groups affording them opportunities for social learning that approximate similar opportunities encountered by their conspecifics in the wild.

In addition, Suddendorf and Whiten’s claims that wild and laboratory-reared chimpanzees have demonstrated an understanding of mental states, even “low-level” ones such as those involving perceptions and intentions, have not gone undisputed. For instance, Tomasello, Povinelli, and their colleagues have presented evidence showing that, in high-constraint experimental research, chimpanzees fail to attribute intentions, to understand seeing as a psychological state, to comprehend declarative gestures, and to reason about attention (for a review, see Povinelli and Bering 2002). In contrast, each of these areas is mastered by children well before their second birthdays (see Flavell 1999). Povinelli does not deny that chimpanzees share with humans an impressive array of social behaviors. Because the two species share such a recent ancestry, there should be few behavioral classes that are altogether unique to humans. But according to Povinelli’s “reinterpretation hypothesis,” the vast majority of complex social behaviors evolved before human psychological systems were around to interpret them in terms of underlying causal states (Povinelli et al. 2000; Bering and Povinelli 2003). Only after such a representational capacity evolved were these ancient behaviors reinterpreted by appealing to such things as the intentions, beliefs, desires, and knowledge states promoting them.

This model implies that the neurological systems supporting intentionality and mental state attribution evolved rapidly (perhaps even as a saltation), finding no precedent in the cognitive hardware of the common ancestor of humans and chimpanzees. In other words, the ability to detect the existence of mental states, and to use these states in order to predict and explain the behaviors of the self and others, might not have evolved until sometime after humans and chimpanzees last shared a common ancestor. This is not simply an assumption made in the absence of evidence of a chimpanzee theory of mind (cf. Fouts et al. 2002). Most of the recent data garnered from high-constraint experimental studies, which have permitted investigators to carefully differentiate between chimpanzees’ ability to learn about the statistical regularities of experiments (i.e., association learning) from their capacity to reason about unobservable mental states, strongly supports this theoretical position (Povinelli and Bering 2002).

Admittedly, this field of research is not entirely resolved. Recently, Hare and his colleagues (Hare et al.

2000a, 2000b; Hare 2001) have argued that these experimental paradigms possess little external validity in that they typically involve humans cooperating with chimpanzees to help the latter obtain desirable food rewards. In that natural chimpanzee ecologies are characterized by intense competition between individuals for access to scarce resources such as food, these designs may not adequately tap the sociocognitive abilities of chimpanzees. Although preliminary experimental findings of metarepresentational abilities in chimpanzees were indeed reported for a design in which conspecifics were pitted against each other in competition for food rewards (Hare et al. 2000a, 2000b), these findings have since failed extensive replication attempts (Karin-D’Arcy and Povinelli 2003). If the available data are any guide to the true nature of chimpanzee minds, therefore, then the theory of mind system should currently be classified as a probable, although not definitive, human cognitive specialization subserved by neurocognitive mechanisms occurring by evolutionary innovation, or perhaps quite by chance (Gould 1991; Preuss 2001; Bering and Bjorklund 2005).

Human social cognition as a developmental system

Relatedly, some investigators, such as Baron-Cohen (1995) and Leslie (1992), argue for a modular view of the theory of mind system, wherein the ability to attribute mental states is enabled by a domain-specific module specially dedicated to serving this role and which is mostly limited to human cognition. Some theorists believe that any meaningful effects of enculturation in the domain of social cognition could occur only insofar as some critical aspects of the neurological structure recruited by the module are present in the cross-fostered species. For example, upon weighing the possible effects of enculturation on chimpanzee cognition, Povinelli (1996 p. 180) writes:

If mere exposure to the conventions and material culture of humans can transform their understanding of others so profoundly, then we might no longer wish to entertain the idea of dedicated cognitive modules that evolved explicitly for the purpose of generating inferences about the mental states of others. If chimpanzees (and other nonhuman primates) normally do not possess the cognitive abilities that modularity theorists envision as being controlled by specialized, evolved brain modules, but if enculturated chimpanzees do, then obviously the underlying neural systems subserving theory of mind in humans did not originally evolve for that purpose. If true, our neurobiological account of theory of mind would need to be recast in terms of the evolution of developmental systems that retain a high degree of plasticity in the face of different epigenetic environments.

In fact, most modularity theorists focusing on the area of theory of mind, particularly Karmiloff-Smith (1992), take pains to articulate that a modular account implies neither the absence of maturation of the system nor a resistance to the effects of the social environment. In other words, hu-

man social cognition is an emergent property that is probabilistic, rather than deterministic, in nature. The important question in relation to the enculturation issue is when in evolutionary history the earliest components of the module first appeared, not necessarily what role these components initially served (they could have operated quite independently of the module prior to its adaptive organization), or even whether these components were explicitly selected for. Suddendorf and Whiten (2001) claim that the neural mechanisms subserving intentionality and secondary representation extend back to the time of the common ancestor of modern humans and chimpanzees: "It appears implausible that [such abilities] can develop without a specialized neurocognitive apparatus having evolved to implement them. It seems to us unlikely they could appear *de novo*, just through human influence" (Suddendorf and Whiten 2001, p. 644).

This may only seem unlikely, however, as a result of the authors' interpreting the empirical literature in the manner that they have. If, as I believe they have done, Suddendorf and Whiten have overinterpreted the available data, and great apes' understanding of intentionality is in reality normally nonexistent, then in fact only humans can be expected to have any dedicated neural circuitry in this domain and it may actually be a matter of such representational abilities appearing "*de novo*" in enculturated great apes. Such neural specialization is likely developmentally based, yet given the wide range of conditions under which intentionality and, later, metarepresentation are expressed in humans (e.g., see Lillard 1997, 1998; Schwanenflugal et al. 1999), it is probably highly canalized as well.

This does not mean, however, that the environment does not serve a critical role in the expression of these representational devices or in the construction of their neurobiological underpinnings. To the contrary, the social environment is an integral part of the developmental system, where individual organisms inherit not just a species-typical genome, but also a species-typical social environment (Bjorklund and Pellegrini 2002). With regard to social cognitive abilities, this idea has best been articulated by Tomasello (1999). According to Tomasello, the experiential social regularities (e.g., joint attention and triadic interaction, bidirectional discourse, being treated as an intentional agent with goals and desires) attending normal human development serve to endow children with abstract causal representational abilities in predictable and recurrent ways. This might occur by way of such species-typical social experiences both helping to build, and then subsequently activating, specialized neural systems underlying these abilities that have come to "expect" such input.

But what happens when such regularities simply do not occur, occur at the "wrong" time, or occur too often? Might developmental events such as deprivation, impoverishment, early stimulation, or atypical rearing histories alter – or, in the case of other species, induce – the phenotypic expression of systems devoted to mental state attribution? It may be unethical to directly address this issue with either humans or chimpanzees by manipulating critical event

thresholds and then assessing their impact on cognitive development (for alternative approaches to chimpanzee enculturation, see Savage-Rumbaugh and Lewin 1994; Fouts 1997; Matsuzawa 2003). The few naturally occurring cases in which children have been found in social isolation, such as the case of the "wild boy of Aveyron," an adolescent discovered to be living alone in the French wilderness at the end of the 18th century (Lane 1976; Hunter 1993) are notoriously difficult to interpret. Children that have experienced extreme social impoverishment might have exhibited congenitally defective social skills, which would have existed independent of their upbringing. Indeed, such abnormalities might have even contributed to their atypical social experiences. For example, parents unable or unwilling to invest in autistic children might have been prone to neglect or abandon them (e.g., Carrey 1995). Likewise, recent proposals to rear chimpanzees in human homes under controlled conditions have been met with controversy, mainly because it requires that a large enough sample of animals be forcibly removed from their mothers and systematically exposed to the social living conditions of human children.

Epigenetic pathways toward atypical phenotypes

Although there have been no controlled studies done on the effects of atypical socialization on the expression of representational abilities associated with social cognition, the bidirectionality of developmental events and phenotypic expression in other domains, such as aggression, sexual behavior, species-typical vocalizations, and sensory-perceptual systems, have a long history of systematic investigation. Research dealing with the effects of early atypical experience on later functioning involves charting epigenetic pathways, or establishing the bidirectional relationships between genetic substrates and particular experiential effects in the phenotypic expression of morphological and behavioral traits. Developmental psychobiologists have taken great strides toward this end, and it is now possible to: (1) identify several specific developmental experiences (e.g., what are the critical event variables that influence genes in the production or inhibition of behavioral expression?); (2) quantify such critical experience (e.g., just how much of this critical experience is required to alter psychological structures and behavioral form?), and; (3) track the developmental relationship between the temporal occurrence of these experiences and their subsequent expression (e.g., when, precisely, are organisms most sensitive to the presence of such critical events, and when can we expect to see their effects?) (Lickliter and Berry 1990; Gottlieb 1996).

For example, Als (1995) has argued that premature infants encounter species-atypical stimulation during sensitive periods of (normally) human prenatal development. Indeed, life-sustaining hospital environments have been associated with a corpus of later problems, such as lowered IQ, impulsivity, and attention deficits. In related research, Gottlieb (1980) isolated ducklings, while still in

the egg, separated them from their mothers, and treated their vocal chords so that they were unable to produce any sound. He found that, unlike a control group, the animals were just as likely to approach the maternal calls of an alien species after hatching as they were their own.

In evolutionary terms, the effects of such atypical experiences are negligible as long as they are isolated to a single generation. Interestingly, however, it may take surprisingly few generations being exposed to atypical developmental histories to produce genuine changes in genomic structures reflecting adaptations to such events. Baldwin's (1896) eponymous mechanism of evolutionary change involves the differential success of individual organisms within a population gaining a reproductive edge through engaging in novel behaviors. The heritability underlying such behavioral plasticity means that subsequent generations, subjected to the same environmental stressors, will similarly be more likely to propagate their genes to the next generation. These intergenerational processes of genetic expression will occur until the behavior loses much of its original plasticity in the face of recurrent environmental stressors eliciting it. That is, because the genetic potential to adapt to specific predictable conditions in the environment becomes essential for the organism's survival, the heritability for this behavioral trait drops to floor values. At this point, the behavior, which may also influence genetic expression in other domains, becomes a standardized adaptation in the species supported by specialized psychological programs. So far, there is only indirect support for some of the general tenets of the Baldwin effect, mostly in the area of morphological change rather than behavioral (and thus psychological) change (e.g., Waddington 1975).

Experimental cross-fostering in macaques (*Macaca mulatta* and *M. fuscata*): an analogue to the enculturation of great apes?

Such findings seem to shed light on the mechanisms by which experiences encountered during early development may ultimately be translated into evolutionarily salient events. Another important source of information especially relevant to the enculturation hypothesis is the cross-fostering literature, and particularly that subset of the cross-fostering literature in which the phylogenetic relationships between the two test species are known. In most cross-fostering experiments, young organisms of one species are reared by adult members of another species, and oftentimes with heterospecific age-mates as well (Owren and Dieter 1989). If the phylogenetic relationship between the two species is too remote, parental rejection is likely to occur. Therefore, cross-fostering research most often involves exposing young organisms of one species to the developmental experiences of a closely related species. The general question explored by such research is whether, by exposing these young organisms to the environments of another, genetically similar species, they come to display behavioral characteristics more similar to the

species that raised them than to their own. This approach can answer a number of important questions, including the extent to which particular behavioral phenotypes characterizing a species (which are often adaptations) are resistant to the effects of environmental change, even when those changes involve being confronted with experiences that are typically encountered by a closely related species.

Several cross-fostering experiments have been done with nonhuman primates, most of these involving two macaque species: rhesus macaques (*M. mulatta*) and Japanese macaques (*M. fuscata*). These species are relatively numerous in research laboratories, and are used in cross-fostering research largely because of their availability. In addition, these species differ from each other in several important ways. For instance, they produce distinctly different patterns of vocalizations, e.g., young rhesus monkeys produce both coos (used mainly during affiliative interactions) and gruffs (used mainly during aggressive encounters), while Japanese monkeys produce coos almost exclusively (Seyfarth and Cheney 1997). Therefore, rearing infants of both macaque species with heterospecifics can determine the relative impact of social learning on the production of such species-typical vocalizations.

Such experiments have produced mixed findings. Owren et al. (1993), for example, found that the species-typical vocalizations of Japanese macaques were not modified by cross-rearing (i.e., they continued to produce coos almost exclusively), while cross-fostered rhesus macaques produced more coos than those raised by normally reared subjects. Seyfarth and Cheney (1997) have therefore suggested that affiliative vocalizations might be more modifiable by social experience than alarm calls (at least in Old World primates). It may not only be the functional characteristics of the vocalizations, however, but also the species emitting them, that determines whether particular calls can be modified by early social experience. In earlier research, for example, Owren et al. (1992) reported that the food calls of rhesus macaques remained unchanged by cross-fostering while those of cross-fostered Japanese macaques came to resemble rhesus vocalizations (see also Masataka and Fujita 1989). The fact that this is the opposite pattern from that seen in Owren et al. (1993) may demonstrate the differential impact of atypical rearing experiences on different behavioral traits, even those within the same behavioral class, such as vocalizations. If, as many developmental researchers believe, the theory of mind system consists of separable, interrelated, representational mechanisms (see Flavell 1999), then it may be possible that these mechanisms might not possess the same degree of developmental equipotentiality for human-reared great apes. Some aspects of the system, for example low-level aspects such as an understanding of attention, intentions, and perception, might be expressed under human rearing, whereas others, such as an understanding of beliefs and knowledge, remain unexpressed in great ape cognition regardless of developmental history.

Another cross-fostering study using *M. mulatta* and *M. fuscata* focused on the development of visual preferences for pictures of seven different macaque species

(Fujita 1993). Young infants from these two species were either reared by humans with conspecifics or heterospecific peers, or cross-fostered between the two species. The monkeys were trained to press a lever to see pictures of macaques, and the findings were that subjects from each group preferred to look at the pictures of rhesus macaques over any other species (even their own, in the case of Japanese macaques). Some species, therefore, might develop preferential biases toward heterospecific physical characteristics and behaviors in response to being cross-fostered. Such biases may, in turn, influence processes of socialization and attention playing a crucial role in the development of other cognitive abilities. [Indeed, in related findings, Tanaka (2003) found that adult chimpanzees that had been reared by humans preferred pictures of human faces over chimpanzee faces.]

Although macaque evolution is notoriously complex and much remains unknown about the phylogenetic relationships between different clades (Eric Delson, personal communication, 6 February 2003), there is evidence that Japanese macaques diverged from an ancestral rhesus population (Melnick et al. 1993). This would suggest that, of the two species *M. mulatta* and *M. fuscata*, the former is the more conservative. Although the findings are far from unequivocal, the cross-fostering research shows that the developmental systems of Japanese macaques may be more sensitive to early social experiences than those of rhesus monkeys. At least in the development of species-specific food calls and visual preferences for conspecifics, cross-fostered Japanese macaques, the more derived species, displayed behavioral patterns characteristic of rhesus macaques, the more conservative species. What this means is unclear. What it may imply is that the potential for developing the underlying psychological programs governing such behavioral patterns in rhesus monkeys remain intact in Japanese macaques, and are instantiated in response to social conditions, which were present in the ancestral environment. Importantly, these social conditions may be similar to those encountered by modern day rhesus macaques. If so, then it is not so much that Japanese macaques acquire new behavioral patterns of a distinct species, but rather that they fail to develop the derived behaviors of their own.

Considering that most physical anthropologists and evolutionary biologists view chimpanzees (*P. troglodytes*) as a fairly conservative species, possessing many of the behaviors and physical characteristics of the common ancestor of humans and chimpanzees, the enculturation hypothesis should be clarified to account for how this phylogenetic relationship might bear on the actual mechanisms by which there is a phenotypic expression of species-atypical traits through atypical ontogenies. For example, given their evolutionary relationship, is it more likely that chimpanzees, when reared under human-like social conditions, will exhibit human-like social cognition? or that humans, when reared under chimpanzee-like social conditions, will exhibit chimpanzee-like social cognition? The former scenario would imply that there was considerable plasticity in the developmental systems of the common ancestor, a

plasticity that is retained in modern day chimpanzees. The critical assumption in this scenario is that a certain set of precursory mental representational capacities is present, but normally not activated, in chimpanzees and can be potentiated when bombarded with human-typical social experiences. The critical assumption also holds that these “latent” competencies in chimpanzees have satisfied some threshold level that can be potentiated.

One possibility of this scenario is that perhaps the common ancestor of chimpanzees and humans possessed aspects of the system, which were then “sloughed off” in chimpanzees but “exacerbated” in humans during subsequent speciation. This would be similar to Povinelli and Cant’s (1995) interpretation of gorillas’ failure to pass mirror self-recognition tests while orangutans succeed – the common ancestor of the two species possessed a self understanding more like orangutans, the authors claim, than gorillas. According to Povinelli and Cant, the rudiments of a self-concept emerged in response to the demands of an arboreal lifestyle imposed on a large-bodied ancestral ape species; those individuals that could plan their movements in the tree canopy in advance of their actions would have had selective advantage over those that failed to evolve this representational system. The authors speculate that, at some point in the species evolution, the gorilla lineage underwent a heterochronic shift allowing for more rapid physical growth in order to accommodate a speciation characterized by an increased terrestrial lifestyle. Subsequently, the cognitive developmental systems underlying the emergence of a self-concept, designed for life in the trees, were reorganized, so that the capacity was not normally expressed under the typical ontogenetic conditions of gorillas.

Another possibility is that there was some form of selection for aspects of the intentionality system during the time of the human–great ape ancestor, and that these aspects were recruited or reorganized in such a way that an understanding of intentionality became standardized in the human species while remaining absent in great apes.

If, however, it is more likely that humans reared under chimpanzee-like social conditions (which, according to the position advocated in the current article, involve the absence of representationally mediated social behaviors, such as natural language) are more likely to display chimpanzee-like social cognition, all we must assume is that the absence of those social regularities tied to the cognitive evolution of the intentionality system, as well as its normative expression in children during individual development, have caused the organism to revert back to the phenotypic expression of the ancestral form in the face of an ancestral social environment.

On premature assertions of the effects of human enculturation on great ape cognition

Unfortunately, current knowledge of the developmental systems underlying the phenotypic expression of representational capacities is very limited. Researchers have iden-

tified neither the critical environmental sources fostering human social cognition, nor discovered the dynamical equations by which infants' brains, at around 9 months, become sensitive to the intentional and perspectival dimensions of others. Nor, for that matter, does the current literature clarify how infants' brains become children's brains, capable of metarepresentation and other forms of higher-order reasoning. Although the development of metarepresentation is influenced by environmental effects, for example by the number of siblings a child has (Perner et al. 1994; Peterson 2001), or the type of discourse solicited by the parents (Ruffman et al. 1999), it is unclear whether it is caused in any way by such effects. If experiences do exert any causal influence, nature has been extraordinarily liberal with the range of human social environments leading to intentionality and metarepresentation. Also, the mechanisms by which representational competencies map onto neural organization is not currently well understood, and the search for those parts of the brain responsible for a theory of mind have been underway for years (see Gallagher and Frith 2003).

Nevertheless, several scholars continue to claim that closely related species, when reared under human-like conditions, will develop a cognitive representational profile similar to that which is associated with young children's understanding of intentionality. For example, Bjorklund and Pellegrini (2002, p. 215), write, "orangutans and chimpanzees have the requisite cognitive flexibility, when raised in humanlike environments, to develop some critical humanlike cognitive abilities associated with theory of mind." In reference to the effects of language-training on the cognition of great apes, Donald (2000, p. 29) comments, "the enculturation process can successfully uncover and exploit cognitive potential that had remained untapped for millions of years." Premack and Premack (1983) have similarly argued on the effects of language on chimpanzees, in that it creates in them an understanding of abstract concepts. According to Rumbaugh and Savage-Rumbaugh (1996, p. 272), "it seems likely that as the chimpanzee learns the relational demands of language, it is developing neurological networks that resemble those that were basic to human neuroevolutionary trends."

Experimental findings: the limiting role of data on the enculturation hypothesis

To what extent are these arguments, especially those concerning the effects of human enculturation on the social cognitive systems of great apes, merited by the available data? There are several key studies at issue. Tomasello et al. (1993a) found both between- and within-species differences in imitative abilities when testing two groups of children, aged 18 and 30 months, and two groups of chimpanzees, mother-reared and human-reared (i.e., enculturated). Each chimpanzee and child was exposed to demonstrations of novel "goal-directed" actions on objects (e.g., placing sifter on head, making noise with an oil can). For the majority of tasks, the subjects were tested on their abil-

ity to imitate directly following the observed demonstrations, but in some cases they were tested after a 48-h delay.

The results were that for the immediate imitation tasks, the only group that failed to imitate both the means and ends of the previously seen actions was the mother-reared sample. In contrast, the enculturated chimpanzees displayed equivalent imitative competence with the tasks as the human children, who showed no significant difference in ability between ages. Reproduction of both means and ends of a demonstrated, novel sequence satisfies Tomasello's definitional criteria for true imitation, which is said to involve an understanding of the intentional relations between the demonstrator's actions and the demonstrator's goal. In addition to these findings of immediate imitation, the enculturated chimpanzees did significantly better on the deferred imitation tasks than both the mother-reared chimpanzees and the human children. Possible reasons for this, according to the authors, included both a main effect of age (the enculturated apes were, on average, twice as old as the children) on memory capacity and a main effect of task comprehension on delayed trials. Because they were not explicitly instructed to reproduce the actions of the demonstrator for the delayed trials, the children might simply have not understood what was expected of them. Neither explanation, however, can account for the difference in performance on the delayed tasks between the mother-reared and enculturated chimpanzees, nor is there much room for any accounting of the immediate imitation data for these two groups other than that they had something to do with the different histories of the subjects.

Findings of mental state attribution by great apes in other areas of social cognition have been interpreted as reflecting an enculturation effect (see Call and Tomasello 1996). Although the majority of such cases are anecdotal and cannot be properly interpreted, many experimental studies have overlooked critical procedural controls capable of distinguishing between successful performance based on the subjects' sensitivity to the statistical regularities of the testing contexts from genuine mental representational skills (Povinelli et al. 2000; Bering and Povinelli 2003). For instance, Call and Tomasello (1994; see also Tomasello et al. 1997) reported that an enculturated orangutan showed better understanding of referential gesturing than a nursery-reared orangutan of comparable age. Referential gestures, such as protodeclarative pointing, refer to, or are about, something in the environment that the partner is believed to be unaware of. Therefore, comprehending such gestures is said to require an understanding of the gesturer's communicative intent (e.g., "she's trying to tell me where the food is"). From these findings, the authors conclude, "in our view, [the enculturated orangutan] had come to understand human beings as intentional agents who have voluntary control over their behavior and attention and who thus sometimes intend for him to behave in a certain way or attend to a particular location" (Call and Tomasello (1994, p. 315).

However, in both this experiment and in Tomasello et al. (1997), the researchers did not control for the location

of the experimenter's hand and index finger, which more recent research has found are cues used by chimpanzees in making selections between objects in various response choice tasks (for a review, see Povinelli et al. 2003). Chimpanzees are more likely to choose a container physically nearer the experimenter's hand and index finger than they are other containers, even if the experimenter's pointing gesture is clearly referencing a more distal container. For instance, because Call and Tomasello (1994) had only two subjects in their design, and because the experimenter always pointed to the container that their hand and index fingers were nearest, it is unclear whether the enculturated orangutan's performance had more to do with its understanding of the referential nature of the gesture or with its ability to make associations between the experimenter's behavior and the location of the food reward. In addition, although human-rearing might be responsible for either of these developmental outcomes (e.g., the enculturated orangutan's experiences with humans might make it better able to form associations dealing with human behavior), there is also the possibility of individual differences between the two subjects irrespective of their rearing histories.

Other studies, while arguing for an enculturation effect on the social cognitive systems of great apes, have not provided a direct comparison between enculturated and mother-reared subjects (e.g., Bering et al. 2000; Bjorklund et al. 2000, 2002). The only direct evidence of an enculturation effect on great ape's understanding of intentions is found in the results of Tomasello et al. (1993a), Call and Tomasello (1994), and Tomasello et al. (1997), each of which made a comparison between these groups. And, as noted, the latter two studies contained several methodological problems, making it hard to interpret the findings.

Findings from other studies comparing the two groups have failed to support the enculturation hypothesis (Call and Tomasello 1995; Call et al. 2000). In a study by Call et al. (2000), for instance, enculturated and nonenculturated chimpanzees were presented with an object choice task in which the subjects were asked to discriminate between the communicative cues given by two experimenters – one (the “knower”) who saw a food reward being hidden beneath one of two opaque containers versus one (the “guesser”) who had his back turned during the hiding event – on the basis of the experimenters' epistemic status. A large occluder in place during the hiding event prevented the subjects from observing which of the two containers held the reward. In one condition (two-experimenter test), the knower was also the person who baited the food containers, while in a different condition (three-experimenter test), a third experimenter baited the food while the knower looked on. In both cases, the occluder was removed after the hiding event and the guesser turned around to face the subject. Both experimenters then stared at the subject's face until they gained its attention. They then transferred their gaze to one of the two containers, with the knower always staring at the correct container and the guesser always staring at the incorrect container.

After 10 s of looking at their predetermined locations, the knower and the guesser simultaneously pushed a platform upon which the containers rested in front of the subject for the ape to make its choice.

The findings were that, for the two-experimenter test, the enculturated chimpanzees outperformed the nonenculturated chimpanzees, choosing the baited container at above chance levels. On the three-experimenter test, however, the performance of both the enculturated chimpanzees and their laboratory raised peers fell to below chance levels, suggesting to Call et al. (2000) that the enculturated chimpanzees had been using some overt discriminative cue on the two-experimenter test (e.g., “pick the person who manipulated the food”), and not an understanding that the knower's gaze was about the location of the reward. The authors conclude, “we thus think that no matter how skillful chimpanzees may become at ‘reading’ the social behavior of others...the understanding of the communicative intentions of others, and the understanding of what knowledge another individual does and does not have – both products of an understanding of others as intentional beings – is not something that even human enculturation can instill in nonhuman primates” (Call et al. 2000, p. 33).

In other works, also, Tomasello periodically attenuates his original stance on great ape enculturation, claiming instead that enculturated great apes undergo a “socialization of attention” by their frequent interactions with humans, and thus learn to attend to human behaviors in ways that allow them to engage in social learning more effectively than laboratory great apes, while their species-standard representational capacities remain unchanged (see also Call and Carpenter 2003). “While human-raised apes learn something more about the triadic nature of human-like communication...this still reflects an understanding of the [physical] causal agency of their communicative partners, not their intentionality and subjectivity” (Tomasello and Camaioni 1997, p. 17).

An alternative explanation: the “apprenticeship hypothesis”

In the face of such uncertainty, researchers may wish to re-examine the central questions involved in the enculturation hypothesis and decide whether findings from a single study (i.e., Tomasello et al. 1993a), albeit impressive, are enough to warrant some of the claims being made. For example, as an alternative to the proposal that human-rearing results in great apes' developing an understanding of intentionality, there are other explanations, such as socialization of attention, that are also able to account for data showing that enculturated great apes are better social learners than nonenculturated great apes. For instance, because of their own understanding of intentionality, human caregivers frequently meet the imperative demands of their chimpanzee charges in ways that mother chimpanzees do not. This may result in the enculturated great ape becoming especially attuned to the actions of humans

on objects, both cultural artifacts and natural objects. According to Bjorklund et al. (2002):

A frequent occurrence in the home-rearing environment is that apes encounter problems with objects from cultural surroundings, and human caretakers advance on these scenes by solving such problems for them. The ape, of course, anxiously attends to these events, observing not only the final solution but also the way its caregiver went about resolving the difficulty. Over a succession of similar episodes during the animal's development, humans continually 'tag' the enculturated apes affective and cognitive experiences of problem states, interceding in the ape's behavioral strategies whenever they perceive that their charge is unsuccessfully going about working on a problem. The ape, in turn, comes to associate humans as problem-solving specialists, and potentially learns that observation (and later reproduction) of human actions can reap big rewards.

Thus, in contrast to Tomasello and his colleagues' claims that human enculturation constitutes an epigenetic re-vamping of chimpanzee psychology such that otherwise human cognitive specializations begin to appear, this apprenticeship hypothesis of enculturation holds that human socialization leads mainly to behavioral change in the form of different problem-solving strategies on novel objects. This hypothesis predicts that enculturated great apes will often prefer that humans solve their problems for them, perhaps even soliciting help by holding out an object or tool for their caregivers to handle, not because they are trying to declare a need, but as an imperative demand. Because their extensive experiences with humans in handling their imperative demands builds on the species' natural facility at motoric mimicry as demonstrated by their ability to imitate arbitrary bodily movements (e.g., Cusance et al. 1995), as well as their ability to symbolically encode action patterns for fairly long periods of time as shown by their performance on deferred imitation tasks (e.g., Tomasello et al. 1993a; Bering et al. 2000) enculturated chimpanzees should demonstrate a significantly greater propensity to imitate on problem-solving tasks than mother-reared or laboratory chimpanzees.

Nowhere in this model, however, is it necessary to posit that enculturated great apes have an understanding of the intentional relations between the demonstrator's actions and the demonstrator's goals. Rather, enhanced imitation in enculturated great apes, in which both means and ends of demonstrated actions are copied with fairly high rates of fidelity, occurs because human-reared great apes have learned that this is an effective problem-solving strategy in and of itself. The animals' behavior constitutes true imitation rightly enough; it is Tomasello's definition of true imitation as a marker of intentionality that is construed as being off (see also Byrne and Russon 1998; Heyes 1998; Horowitz 2003).

Findings from Carpenter et al. (1995) seem to support this interpretation. These authors reanalyzed the original videotaped data from Tomasello et al. (1993a) and found that, in contrast to the mother-reared chimpanzees, the en-

culturated chimpanzees were, like the children, compliant during the demonstration session. They tended to spend more time engaged in the experimenter's actions upon the object(s), and to be less distracted by other things in the environment, than the mother-reared chimpanzees. Just like the latter, however, they spent little time checking the eyes or face of the experimenter – something the children did quite often. According to Baron-Cohen (1995), under conditions of behavioral ambiguity, people routinely check the eye region of an actor's face in an attempt to gauge their intentions, a representationally based behavioral strategy that is largely absent in individuals with pronounced social cognitive deficits, such as those with autism (see also Baron-Cohen et al. 2000). This suggests that what the enculturated subjects were learning had more to do with reproducing the specific actions they were witnessing than deciphering the intentions of the demonstrator. Carpenter et al. (1995, p. 233) concluded that, "The overall point is that it is how chimpanzees attend to objects, not specifically to people through looks or gestures, that is the major focus of the enculturation process, and thus it is there that we see the biggest differences between the enculturated and mother-reared chimpanzees."

There are several ways to continue teasing apart these competing interpretations of enculturated great apes' social learning abilities. For example, there should be a systematic comparison between the imitative performance of enculturated great apes when conspecifics demonstrate goal-driven actions on novel objects and their performance when humans are the models. If the cognitive systems of enculturated great apes have indeed been restructured such that others are perceived as intentional agents, then there should be no real difference in their levels of imitative performance in these two cases. It is quite difficult to imagine a plausible evolutionary scenario in which enculturated chimpanzees should develop the ability to reason about mental states in humans, but no other species (including their own). Rather, if it is the case that more superficial changes have occurred, in that great apes reared by humans come to adopt problem-solving strategies that involve attending to and replicating human actions on objects simply because it is an effective problem-solving strategy, then they should be significantly more likely to imitate human than chimpanzee demonstrators. The proper approach to a study of this kind would be a two (enculturated vs nonenculturated) \times two (human model vs chimpanzee model) design with repeated measures on the demonstrator type factor.

Another way to test the apprenticeship hypothesis would be to compare two samples of adult chimpanzees from a laboratory-raised population – one group, the experimental group, would receive special training prior to testing such that human experimenters satisfy a number of their imperative demands with novel objects, whereas the other group, the control group, would receive no such training. According to the apprenticeship hypotheses, the experimental group should outperform the control group on imitation tasks, not because they understand the intentions of the demonstrator, but because they have learned that at-

tending to human behavior on novel objects, and then reproducing that behavior on such objects, results in favorable outcomes. If such effects were found between two comparable groups of laboratory-reared adult chimpanzees, then this would call the central tenets of the enculturation hypothesis (which involve the development of species-atypical neural pathways during human rearing) into question.

As a final example, the original sample of enculturated great apes from Tomasello et al. (1993a) should be tested on a series of different mental representational tasks. If they have indeed developed an understanding of intentionality, then they should demonstrate this ability not only on imitation tasks, but also in other experimental designs capable of distinguishing performances based on conditioning from those demanding the attribution of mental states. If their social cognition has indeed been configured in such a way that they understand others as intentional agents, then enculturated apes should demonstrate this understanding in any controlled experimental procedure where the objective is to reveal an understanding of the intentionality of agents.

Concluding remarks

Although the enculturation hypothesis has found some empirical support, particularly in the area of enculturated great apes' social learning abilities, it is premature to state that human-raised great apes have undergone any meaningful alteration of their species-typical cognition. Many scholars, however, continue to promote the hypothesis, and to view the single experimental study on which it was founded, as *prima facie* evidence of its validity. In addition, those researchers advocating the enculturation hypothesis have not explored the theoretical biology deeply enough. Advocates must explain more clearly how it is that the cognitive and psychological adaptations of humans, a derived species, can come to appear in the cognitive phenotype of a conservative species in response to the latter being exposed to social behaviors that were probably absent in the common ancestor.

Also, enculturated great apes should be tested in a variety of social cognitive domains, not just imitation. If the social cognition of great apes is transformed by their being treated as intentional agents, then the social behaviors of enculturated great apes should reflect this transformation in any domain necessitating an understanding of intentionality and reference. Preliminary evidence of enculturated chimpanzees' failure to understand that seeing leads to knowing has not supported the enculturation hypothesis (Call et al. 2000). Until additional data are collected in other mental representational domains, then the current findings of enhanced imitative abilities in enculturated over captive great apes can be explained by alternative hypotheses. For example, the apprenticeship hypothesis can account for the available data on differences between human-raised and laboratory great apes and does

not require that the former view human behavior as intentional. In conclusion, the evidence that enculturated great apes possess an understanding of others as intentional agents is not there – not yet.

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