
DARWIN'S LEGACY: A COMPARATIVE APPROACH TO THE EVOLUTION OF HUMAN DERIVED COGNITIVE TRAITS

MARCOS NADAL*; LLUÍS BARCELÓ-COBLIJN*;
ANTONIO OLIVERA*; JULIA F. CHRISTENSEN*;
CRISTINA RINCÓN-RUIZ**;
CAMILO J. CELA-CONDE*

ABSTRACT. There is a broad agreement that the most notorious traits that set our species apart from any other, those that define our humanity, include language as a means of communication and mental representation, a highly developed moral cognition, and appreciation of beauty, together with art and aesthetics. The greatest obstacle for research on the evolution of such cognitive traits is the absence of substantial direct physical evidence in the fossil and archaeological records that can ground testable hypotheses. However, we believe that the comparative method provides a powerful tool to overcome this limitation and that it can provide a rich starting point to characterize the evolution of human cognitive apomorphies. In this paper we review the most significant facts derived from the comparative literature relevant to human language, morality, and appreciation of beauty. We use these facts to assemble a tentative picture of their evolution and we discuss possible common underlying processes and trends. Only an integrated perspective can fully account for the evolutionary history of human language, morality, and appreciation of beauty.

KEY WORDS. Darwin, evolution, mind, language, morality, beauty appreciation.

1. INTRODUCTION

Darwin was certainly not the first to propose that current living organisms are the result of an evolutionary process. He was, however, the first to formulate an evolutionary mechanism—natural selection—that integrated knowledge from population dynamics, geology, breeding, and the extensive and meticulous observation of a broad variety of plant and animal life from around the world. The main strength of natural selection was that it could explain complex biological structures as the result of an accumulation of many modifications inherited throughout generations of organisms. Darwin (1859) himself admitted having difficulties conceiving

* Human Evolution and Cognition. Associated group to IFISC (UIB-CSIC), University of the Balearic Islands, Spain.

** Hospital Infanta Leonor. Instituto Madrileño de la Salud, España.

marcos.nadal@uib.es / cjcela@atlas.com.es

that the eye, a good example of complex biological system, with all its functions and features, could be the product of a process so lacking in intention and planning as natural selection. Anyhow, this idea becomes more plausible when founding the explanation of its evolution on small and favorable changes:

Reason tells me, that if numerous gradations from a single and imperfect eye to one complex and perfect can be shown to exist, each grade being useful to its possessor, as is certainly the case; if further, the eye ever varies and variations be inherited, as is likewise certainly the case; and if such variations should be useful to any animal under changing conditions of life, then the difficulty of believing that a perfect and complex eye could be formed by natural selection, though insuperable by our imagination, should not be considered as subversive of the theory (Darwin, 1859, p. 136).

Although inheritance mechanisms were unknown to Darwin, the notion of descent with modification constitutes the foundation of his explanation of the origin of anatomical traits. Moreover, Darwin believed that this scheme could also be applied to understand the origin of functional traits, including complex cognition. We find in his works interesting contributions regarding the evolution of language, morality, and aesthetics, three high-level cognitive faculties that are uniquely human. Our capacities to use language as a representational and communicative instrument, to understand moral judgments and resolve moral dilemmas, and to create and appreciate beauty, appear to delineate the frontier of humanity. However, as Darwin argued, this set of cognitive faculties, that seem to set our species apart from other living animals, including primates, is necessarily the product of descent with modification from the cognition of our primate ancestors.

As Darwin also realized, this cognitive ancestry can be studied by comparing closely related living species. The comparative study of species provides a mean to clarify the phylogenetic relations among them and to shed light on the evolutionary history of the traits that characterize them. The comparative method relies on two fundamental methodological tools: The distinction between homology and homoplasy, and the principle of parsimony. A trait is said to be homologous when it appears in two species because it was inherited from a common ancestor, such as the five digits in different species of mammals. Conversely, a homoplasy is a trait exhibited by two species as the result of independent evolutionary processes, like the wings of sparrows and bats. The principle of parsimony is primarily used as a means to organize evolutionary lineages of closely related species, especially in reference to traits that are not reflected in fossil remains. This principle states that if a trait appears in two closely related species, such as human beings and chimpanzees, or human beings and

Old World monkeys, it can be assumed to be a homology. That is to say, the presence of the same character in these species is more likely to be the result of the inheritance from a common ancestor than of its independent evolution in both species.

In this paper we will not to review Darwin's original contributions to the study of the evolution of language, morality, and aesthetics. Rather, we will summarize current findings in the comparative literature regarding these cognitive faculties. Implementing the principle of parsimony, we will sketch some basic features of the evolutionary histories of these three remarkable and complex cognitive faculties. We will conclude by attempting to extract common aspects underlying those histories and offering a characterization of the manner in which the human mind evolved.

2. THE COMPARATIVE APPROACH TO LANGUAGE

Scholars approaching the issue of language evolution have usually accepted either that language is special to humans and it appeared suddenly, or that language is special to humans and it appeared progressively. The former view usually entail the often implicit assumption that language is a monolithic faculty. Instead, the latter tends to posit several evolutionary steps until an organism reaches 'languagereadiness,' in Corballis' (2002) words. The second option has two possible readings:

- a) Human language is a distinct and discrete faculty that evolved because selective (possibly environmental and social) pressures acted on it (Pinker 1994).
- b) Natural selection endowed some of our ancestors with diverse representational and communicative abilities at different points in our evolutionary history, most of which were inherited by current human beings. Modern human language emerged in virtue of the reorganization of this unique combination of elements.

In any case, approaches to language evolution should be able not only for communicative behavior, but also for the language-related abilities and mechanisms that underpin such behavior. Therefore, we will draw a threefold classification: language perception abilities, language learning abilities and language computation abilities. The modern human faculty of language requires all of them for ontogeny and its natural use. The comparison of humans and other animals on tasks designed to assess those abilities has afforded data that can be used to delineate a cladogram like the one presented in Figure 1 at the end of this article, where the different abilities are ordered by chronological appearance. The comparative studies reviewed below support the aforementioned second reading.

2.1. LANGUAGE PERCEPTION ABILITIES

Different human languages exhibit different rhythmic patterns, and human adults are able to distinguish between linguistic rhythms. A question that has received much attention is whether human infants are also capable of this. For instance, Nazzi and colleagues (2000) showed that five-months old children were able to discriminate rhythmic classes when languages were very different (English vs. Japanese) and when languages were of the same group close to their native language (British English vs. American English, or British English vs. Dutch). Instead they failed to distinguish within foreign languages that did not belong to their rhythmic group (Italian vs. Spanish) and also failed when two languages were not equally familiar (German vs. Dutch).

These results were traditionally interpreted as showing that natural selection had endowed our species with special mechanisms that facilitate language perception and acquisition. However, recent experimental data have revealed that this ability originated several million years before the appearance of hominins. Tincoff and colleagues (2005) have shown evidence that cotton-top tamarins are also capable of discriminating languages according to their rhythmic patterns. They do, however, show subtle differences. For instance, their performance is poor when languages belong to the same rhythmic group (American English vs. Dutch), though they achieved positive results when languages belonged to different groups. In accordance with the principle of parsimony, we could hypothesize that the ability to discriminate human language rhythmic patterns did not appear independently along the human and tamarin lineages. Rather, it is probable that their common ancestor, which lived some 40 million years ago, already possessed this capacity. But even more surprisingly, it has been proved that the common mouse (*Mus*) has the same ability to discriminate rhythmic classes as tamarins (Toro, et al. 2003). It is worth noting that when the stimuli were played backwards, a condition in which relevant acoustic information is lost, none of the tested samples—human newborns, tamarins and mice—were able to discriminate between rhythms.

These facts lead to the conclusion that more than 70 million years ago, the ancestor of *Mus* and primates already exhibited this ability. It is difficult to ascertain why a 70 million year old extinct mammal should be able to discriminate between human languages. Most probably, human language production and comprehension relies heavily on general perceptual and cognitive processes that are common to current primates and other mammalian species. This is also true of *categorical perception*, another property of human language that has been shown to be in reach of other mammals. It has been proved that both *Chinchilla* and tamarins distinguish between alveolar plosive consonants, namely [t] and [d] (Kuhl and Miller 1975).

2.2. LANGUAGE LEARNING ABILITIES

Although it is well established that human memory plays a fundamental role in our cognition and language, experimental results suggest that this is not what makes our species different. For instance, Kaminski and colleagues (2004) showed that dogs exhibited good memory abilities in word learning tasks related to nouns. In addition, it seems that they can also integrate information about the identity (what) and the location (where) (Kaminski, et al. 2008) of the objects referred to by the nouns.

In relation to the statistical ability that human infants exhibit at the age of 8 months when learning words, acoustic cues or rules, Hauser and colleagues' (2001) experiments with tamarins demonstrated that the ability to segment continuous speech into discrete words is not a uniquely human trait. Tamarins showed evidence of discriminating between sequences of syllables that differed only in the frequency or probability with which they occurred in the streams of stimuli. Humans seem to have extended these abilities additionally and therefore can perform tasks with a higher level of complexity of serial order.

It was later argued that that analysis was not adequate for certain linguistic structures that involve adjacency of the elements. This led Newport, et al. (2004) to verify whether tamarins could learn statistically non-adjacent dependencies. Results showed that these primates were unable to acquire patterns involving consonants but that they were rather proficient with patterns involving vowels, even when the vocal phonetic regularities were non-adjacent. The fact that tamarins seem to be unable to produce stop consonants could be part of the explanation of these results.

With regards to rule learning, Marcus and colleagues (1999) showed that infants are capable of extracting both simple transitional probabilities and simple algebraic rules from sequences of speech, as demonstrated by studies using ABB grammars. An experiment with tamarins carried out by Hauser, Weiss and Marcus (2002) evidenced that tamarins were also able to extract sequential patterns. However, evidence from 2004 led the authors to suggest that the fact that they cannot learn language, and that they cannot extract recursive patterns, is due to their inability to extract and generalize abstract templates (Fitch and Hauser 2004). In consequence, they advocated Chomsky's approach regarding the abilities to both maintain a lexicon, form semantic representations and link them with syntactic representations.

2.3. LANGUAGE COMPUTATION ABILITIES

These abilities are related to cognitive procedures required in order to produce and parsing well-formed linguistic structures. The Chomsky Hierarchy establishes four levels of grammars, which maintain an inclu-

sive relation, as a Russian-doll. Generativists usually consider that only our species has reached the highest level of linguistic structuring. Fitch and Hauser (2004) aimed to test this assumption in an experiment that faced tamarins with recursive and non-recursive grammars. In line with Hauser, Chomsky and Fitch's (2002) view of *recursion* as the only one cognitive element that makes unique human faculty of language, Fitch and Hauser's (2004) results showed that tamarins were not able to process recursive patterns. However, further research has proved that other animals can master a Context-Free Grammar. For instance, it has been shown that starlings (*Sturnus vulgaris*) are able to recognize and master recursive patterns (Gentner, et al. 2006). In this regard, Marcus (2006) noted that whereas tamarins in the Fitch and Hauser's (2004) study were subjected only to a brief exposure, starlings had undergone an intensive training regime. Thus, singing recursive structured songs is not their natural condition. Notwithstanding, the fact that they have such a possibility raises the question as to the situation in which they use recursion naturally. Could it be in relation to cognitive maps (Gallistel and Cramer 1996) as other birds do?

There is yet another important ability that links structures with meaning. However, in this case there is no evidence suggesting that other animals may also possess it (Rosselló, 2006). We are referring to duality of patterning, the linguistic feature proposed by Hockett (1960) that makes it possible to create sets of phonemes (which are cognitive entities) and then combine these sets to construct meaningful words. Okanoya's (2007) recent work on song-birds suggested that wild finches (*lonchura striata*) could have similar phonological devices to those of humans. These could have been lost in domestic finches (*lonchura striata* var. *domestica*), domesticated in Japan 250 years ago. But this is still far from duality of patterning in Hockett's sense. For now, it seems that the union of mentally structured sounds into meaningful units (morphemes) and their later combination into words is only within reach of *H. sapiens*, appearing, thus, roughly 200 000 years ago.

2.4. CONCLUSIONS

We have reviewed evidence that shows that categorical perception, rhythmic discrimination and language discrimination are abilities shared by humans, non-human primates and rodents. The principle of parsimony leads us to believe that they appeared at least before the split between rodents and the rest of mammals (aprox. 70-80 Mys ago). Additionally, learning words and linking them with entities and locations are not unique to humans. Neither discriminating within syllables nor statistical learning seem to be completely specific for humans either. At least patterns based on vowels are discriminated by tamarins and their extraction of

patterns is unquestionable. Finally, other primates are capable of mastering serial linguistic grammars.

However, as we have also noted, there are certain human peculiarities. For instance, whereas tamarins perceive non-adjacent relations between vowels, humans can perceive such relations based on consonants and, moreover, between distant elements within clauses. In other words, in this regard, evolution in humans has improved their skills for statistical learning and extracting templates. We have also noted that humans and not other primates are able to master recursive grammars. Finally, human language seems to be the only natural system characterized by duality of patterning.

This set of results suggests that far from natural selection leading to a broad novel set of cognitive mechanisms to support language, it endowed humans with a language that profited largely from pre-existing mechanisms that were previously engaged in non-linguistic processes. The evolutionary history of each of these mechanisms is unique, they seem to have appeared at different times throughout the evolution of mammals and primates specifically, and probably owe to very different selective pressures. Hence, human language evolved by recruiting and refining common primate cognitive mechanisms and the appearance of—at least—two novel features: recursion and duality of patterning.

The cladogram presented in Figure 1 deserves some caveats. There is still a need for research to eliminate possible homoplasies from the cladogram. We still do not know whether chimpanzees—or other great apes—are really able to distinguish rhythmic patterns or statistically extract rules. In the case of categorical perception, since it is present in very different species—rodents and monkeys—it seems reasonable to think that such abilities emerged at least at the time of the split between rodents and the common ancestor of primates. Maybe the most intriguing question from the linguistic point of view is the possible use that starlings make of recursion—if any—and the fact that duality of patterning still remains as a special (maybe the most special, since it links phonemes to meaning) language-related ability, which still remains undetected in other extant animal species.

3. THE COMPARATIVE APPROACH TO MORALITY

When Charles Darwin wrote *The Descent of Man, and Selection in Relation to Sex* (1871) he was probably the first scientist to understand morality as a logical evolutionary product, a conception which is congruent with his revolutionary vision of the evolution organisms as a biological continuum (Darwin 1871). More importantly, the idea of biological continuity supports Darwin's predictions about how the presence of social instincts in

any species would be the first step or requisite for the development of a "moral sense." Hence, from this evolutionary point of view, no disruption between the morality of *Homo sapiens* and non-human primates' social instincts is expected. Nevertheless, something is missing in this puzzle. Even Darwin acknowledged that "(...) of all the differences between man and the lower animals the moral sense or conscience is by far the most important" (Darwin 1871, Chapter III). Thus, it must be stressed that humans have developed a wide range of implicit/explicit moral rules, in the form of social and "spiritual" duties and virtues, national and local laws which are in constant interaction with our daily intuitive moral judgments, constructing, in sum, hyper-complex moral systems. In spite of this, it seems appropriate to ask if morality actually is a distinctive characteristic of human kind. Clearly, we are not dealing with a simple "yes or no" question.

The comparative approach to morality will require analyzing the underlying psychological processes and capacities level by level, in order to be able to actually classify non-human animals' "moral behaviors" as analogous or homologous to those of humans. Indeed, many non-human primates have evidenced human-like methods to deal with the conflicts inherent to social life. Specifically, behaviors like reciprocity, reconciliation, consolation, conflict intervention or mediation have been well documented in several comparative studies, to such extent that these behaviors have been considered the "building blocks" of morality (Flack and de Waal 2000). Each of these so-called blocks appears to include different cognitive and affective mechanisms which seem correlated with the complexity of the behavior and, interestingly, the taxonomical place of the genre. In what follow we are going to give an account of the different behavioral traits identified in comparative research as being related to moral behavior.

3.1. MORAL BEHAVIORS

Sharing. Food sharing in non-human primates has been documented in chimpanzees (de Waal 1997), bonobos (de Waal and Lanting 1988), orangutans (Edwards and Snowdown 1980), capuchin monkeys and cotton-top tamarins (Hauser, et al. 2003). Although the psychological mechanisms that make one individual voluntarily allow another individual to take its food are not yet clear, this behavioral particularity has been studied in the field of reciprocal dynamics and has been functionally explained as a way of social dominance and direct competition, an alternative method to regulate interactions and reduce aggressive encounters (Flack and de Waal 2000), so to speak. Nevertheless, food-sharing among unrelated individuals is not a common practice within the animal kingdom, and it

is usually motivated by mutualism (Brown 1983), when cooperators receive immediate "selfish" benefits of the interaction.

Fairness. Non-human primates appear to be sensitive to effort (van Wolkenten, et al. 2007) and capable to detect and punish cheaters. More importantly for our purposes, this aversion towards inequity can hardly be explained without the cognitive capacity of individual recognition (Hauser, et al. 2003) and the feeling of a punitive/retributive emotions toward inequity (Brosnan and de Waal 2003; de Waal and Berger 2000; Nichols and Mallon 2006). However, the widespread presence of kin-mutualism manifestations among non-human primates dramatically looses in distinctiveness when compared to their lack of outside-kin and non-immediate cooperation interactions (reciprocal altruism; Trivers 1971), all common practices in human societies. This fact was considered by Stevens and Hauser (2004) who believe that there are three main cognitive prerequisites (or "psychological ingredients") necessary for the occurrence of reciprocal behavior that are uniquely human: (a) Temporal discounting, or the consideration of delayed gratification; (b) Numerical discrimination, or the capacity to quantify, and (c) Learning memory, needed to hold in mind the quality of exchanges (Stevens and Hauser 2004).

Reconciliation. This is a common social behavior among most primates' species (de Waal and Aureli, 1996). This moral block has been associated with some psychological particularities, such as the importance of the "quality" of the relationship—which also implies learning memory and the capacity of individual recognition—which appears to be associated with the likelihood of a reconciliatory tendency. Hence, according to Cords and Aureli (2000) primates take account of the fitness value, security/stability and the compatibility of their relations in order to establish peaceful post-conflict contacts (Cords and Aureli 2000; Manson, et al. 2005). However, although it is not yet clear if such "friendly" behaviors are motivated by empathic concern (as described in the proposal by Cords and Aureli 2000) or if it is just an automatic response motivated by the desire to avoid negative arousal (a possibility also considered by de Waal 2003; 2007), it still seems plausible that variables like familiarity and similarity would in some way "shape" the representations of others' emotional states, making the occurrence of an empathic process more likely (Preston and de Waal 2002).

Mediation and conflict intervention. Here, individuals that intervene do not choose any particular side, a remarkable behavior which is interpreted as the existence of a representation of a "higher" goal—for example, restoring peace—rather than just supporting closer members of their own companions group (de Waal 1982). Obviously, a negative arousal avoidance expla-

nation has to be considered too. Nevertheless, frequently we are tempted to simply translate other primates' behavior into the language of our own mental states (Gomez 2007; Povinelli and Vonk 2003) and to accept the controversial assumption of a non-human primate Theory of Mind (ToM) (Heyes 1998). Again, there is no simple answer to this question. As pointed out by Tomasello and colleagues (2003a), at least some human primates understand *some* psychological states of others, a necessary fact for the study of inter-specie differences and similarities in cognitive capacities (Tomasello, et al. 2003a).

3.2. COGNITIVE AND AFFECTIVE PROCESSES UNDERLYING MORALITY
Inferring from the physical world. It appears that chimpanzees have a far better understanding of causal relations than of arbitrary ones (Call 2005), being able to deduct the physical permanency of objects in space (Hare, et al. 2001), and even of some psychological states related to visual perception of *what others can see or cannot see* (Gomez 2005; Tomasello, et al. 2003c). Apparently, they also have some "proto" abilities of attention and intention (Gómez 2007; Tomasello, et al. 2003c) and certain metacognitive abilities (Call 2005) and of the celebrated Machiavellian intelligence (Byrne and Whiten, 1988; de Waal 1982). All this evidence suggests that we must understand ToM as an inclusive and pluralistic concept, which contains a wide range of cognitive processes.

Theory of Mind. Understanding perception and knowledge implies an understanding, not only of what an agent is oriented to, but also of what she is perceiving, or seeing, in her environment and what she knows from previous encounters with the same environment. It has been suggested that chimpanzees "only" use contextual or behavioral cues instead of understanding perception and knowledge of the agent. Indeed, due to the cognitive limitations of non-human primates it is hard to reject the behavioral-cue explanation for obtained results. Thus, Povinelli and Vonk maintain the view that chimpanzees appear to have representations of the behaviors of others, using behavioral cues to infer "what happens next" in an interaction. They call this first order ToM (Povinelli and Vonk 2003). The authors discuss, that often anecdotic evidence of deception in chimpanzees is used to attribute second order ToM to chimpanzees. Nevertheless, they believe that deception can be explained by first order ToM, e.g., by the use of learned behavioral rules. Tomasello and colleagues (2003b), conversely, maintain that chimpanzees do understand some psychological states. In experimental conditions where chimpanzees were incited to use "behavioral cues" they actually did not, relying rather on their supposed ability to infer mental states. These authors would argue that chimpanzees seem to have an understanding of goals, intentions, perceptions and knowledge of others, but in another degree than humans (Call,

et al. 2004; Call and Tomasello 1998, 2008; Tomasello, et al. 2003b). Humans' cognitive ToM is more complex, involving also the comprehension of false beliefs, possibly the ultimate sophistication of this capacity.

Empathy. Frans de Waal proposed a layered conception of empathy, admitting significant variations of complexity in the different layers (de Waal 2003). His studies suggest that a Perception-Action Mechanism (PAM) evolved from basic responses to environmental and social inputs following the dimensions of "good-approach/bad-avoid". This mechanism was further refined in group living animals as a response to the complexity of their cognitively more demanding environment (Preston and de Waal, 2002). Hence, evolution has "build up" upon this mechanism adding to the PAM three affective/cognitive innovations in progressing complexity: (i) emotional contagion, which is an automatic, immediate, emotional state matching, also described as an "adoption" of the other's arousal/emotional state (de Waal 2007); (ii) cognitive empathy, which implies understanding of what is causing the other individual's emotional state—in other words, an appraisal of the other's contextual/emotional situation—(Preston and de Waal 2002), and (iii) the attribution, which implies the ability to completely adopt the other's position (de Waal 2003). The differences in the complexity associated with each layer are well defined by the authors and help to discriminate the presence of empathic behaviors—and their complexity—within the animal kingdom. Emotional contagion has been documented in a wide range of species, from the big apes to rats and pigeons (de Waal 2007). Conversely, cognitive empathy appears to be exclusive to apes (Flack and de Waal 2000), and it appears to be associated with the cognitively high-demanding moral blocks of consolation, conflict intervention and mediation. For instance, in the case of consolation, there is empirical evidence suggesting that the post-conflict contact rate between a third party and the victim of the conflict is directly correlated to the intensity of the former aggression suffered by the victim (de Waal and Aureli 1996). This relationship is commonly interpreted as a proof of some understanding of emotional states in another individual and, perhaps, of the contextual perspective of the others.

Distinction between self and other. The abilities mentioned above can only be explained if the individual has an understanding of the differentiation between self and other, e.g., the capacity to experiment that the source of vicarious arousal is *other* and not *one-self*. As before, evidence suggests that the ability of self/other distinction appears to be restricted to hominoids (Preston and de Waal 2002) and maybe present in dolphins (Reiss and Marino 2001) in which, curiously, anecdotic evidence of helping behavior has been reported (de Waal and Aureli 1996). One might wonder, about the real implications of such results, but, undoubtedly, methodological

constrains in the self-awareness tests are quite likely to open up for a wide range of speculations. Of course, it seems unlikely that other species can reach a human self-reflexive awareness (Hauser 2001), but the existent data is consistent enough to support an “own body-sense” (Bekoff 2002a, 2002b), understood in the terms of “this is *my* nose and does not belong to other.”

3.3. CONCLUSIONS

It has long been discussed if humans are actually the only living specie that deserves to be considered authentically moral. When the aforementioned facts are taken together they constitute a considerable evolutionary puzzle. The evidence presented above contributes to illustrate the necessity to understand the evolution of morality as a heterogonous and “economic” process. Thus, according to our proposal, whether or not we can call “moral” a chimpanzee, is not the central question. Rather, we consider that different species have developed different versions of psychological abilities—and different levels of complexity in the subjacent processes. To deny this fact would be like denying the concept of adaptation in the organisms’ evolution. Indeed, parsimony has something to say about the fact that our closest biological relatives have developed psychological mechanisms that play a strikingly similar role to ours in their social lives, exhibiting a set of behaviors that are—using Povinelly and Vonk’s (2003) terminology—“suspiciously” human.

From our perspective, it seems very unlikely that these particularities could be explained as biological or “social” analogies. Moreover, we consider it legitimate to hypothesize that at some evolutionary step, after the cladistic separation of hominins and chimpanzees our ancient relatives developed new methods for coping better with an emerging new variety of psychological states (see also Tomasello, et al. 2003b). This does not mean to accept a discontinuity as explanation. Rather, the evidence presented above suggests that our modern and sophisticated cognitive and affective faculties are actually based on more basic mental capacities that we share—as homologous traits—with other primate species and antedate our specie appearance. In sum, from a phylogenetic perspective, we believe that the morality of *Homo sapiens* is a derivate consequence of the development of particular cognitive and affective innovations that emerged over ancient psychological structures adopted to play a new adaptive function, presumably, in the field of social dynamics.

4. THE COMPARATIVE APPROACH TO BEAUTY APPRECIATION

In contrast with language and morality, there are no comparative behavioral studies addressing the appreciation of beauty. Researchers have still to come up with experimental designs that allow comparing human and non-human animals on aesthetic preference tasks. In the meantime, here

we must settle for a different approach. We will first characterize the cognitive and affective processes involved in the appreciation of beauty. Then we will briefly review what is currently known about the neural substrates of those processes. Finally, most of this section will be devoted to detailing, with the aid of comparative neuroscience, the evolutionary history of the cognitive and affective mechanisms that enable our appreciation of beauty.

Chatterjee's (2003) is one of the most influential models of aesthetic preference. The model suggests that, in the case of visual arts, during the initial stage, early visual processes divide the stimulus into simple components, such as color and form, which are extracted and analyzed in different brain regions. In a subsequent stage, intermediate visual processes group certain elements and segregate others to form coherent representations. In late visual stages, certain regions of the stimulus are selected for processing in greater detail. At this moment, information stored in memory becomes active; objects are recognized and associated with their meanings. This visual analysis elicits emotions associated with the aesthetic experience and provides the foundations to formulate aesthetic judgment. This model also includes feedback of information, via attentional processes, from late visual levels and affective systems to early visual processing stages.

Based on the results of four recent neuroimaging studies and the current knowledge of the neural correlates of cognitive and affective processes, it is possible to determine the neural mechanisms underlying Chatterjee's (2003) stages. Affective processes involved in aesthetic preference seem to be mediated by certain regions of the orbitofrontal cortex (Kawabata and Zeki 2004), the caudate nucleus, and the anterior cingulate cortex (Vartanian and Goel 2004). The recognition of the visual stimulus and the attribution of meaning in aesthetic preference seem to be related to activity in the temporal pole (Jacobsen, et al. 2006). The actual decisions required by the experimental settings are mediated by the lateral prefrontal cortex and the frontal pole (Cela-Conde, et al. 2004; Jacobsen, et al. 2006). Finally, there is evidence of top-down enhancement of early visual processes carried out in the occipital cortex (Vartanian and Goel 2004). We now turn to comparative neuroscience to sketch the evolutionary history of the neural and cognitive underpinnings of beauty appreciation.

4.1. VISUAL PROCESSING SYSTEM

As we saw above, the study performed by Vartanian and Goel (2004) revealed that visual processing activity in the occipital gyri was greater when participants awarded high preference ratings. Several studies have shown that throughout human evolution, brain regions involved in visual processing have expanded to a lesser degree than the whole brain (Rilling

2006; Schoenemann 2006), suggesting a trade-off towards cognitive processes which are not directly bound to sensory information. Turning to a finer level of analysis, the retinotopic organization and functions of brain areas involved in early visual processing, known as V1 and V2, are conserved to a great extent in human beings (Orban, et al. 2004). However, certain aspects of the human area V1 are derived. For instance, Preuss and Coleman (2002) found that humans differ from monkeys in certain features related to the cortical representation of the magnocellular system. It seems that some of these features occurred initially in the common ancestors of African apes and humans, while others appeared to have evolved exclusively along our lineage. Given that the magnocellular visual processing stream is involved in the analysis of luminance contrasts, movement, perspective, the relative size of objects and depth perception, it is reasonable to assume that the changes that appeared in this stream had an impact on these perceptual processes.

Whereas homology in monkeys and humans is relatively easy to study in primary visual areas, this becomes increasingly difficult as one moves to higher levels of the visual system. Various studies reviewed by Orban and colleagues (2004) suggest that the ventral and dorsal visual information streams have been transformed to different extents throughout human evolution. Specifically, the areas that constitute the ventral stream, related to the representation and categorization of objects, have experienced a smaller expansion than those that are part of the dorsal stream, involved in the representation of space and the analysis of visual information to organize action (Orban, et al. 2004). Barton (2006) noted that the fact that parietal areas of the dorsal stream receive information only from the magnocellular system, supports the aforementioned notion that cortical representations of information fed by the magnocellular system have been the target of special modifications throughout human evolution. The studies that have shown brain activity in homologous brain regions in humans and monkeys during the perception of symmetry (Sasaki, et al. 2005), the representation of visual objects (Munakata, et al. 2001), and their classification (Sigala, et al. 2002), support the idea that the ventral visual processing stream is relatively conserved in human beings.

4.2. TEMPORAL POLES

Jacobsen and colleagues' (2006) neuroimaging study mentioned above revealed that the task of rating the beauty of geometric visual stimuli is related to greater activity in the left temporal pole than the task of rating other visual features. The authors suggested that the function of this region was to generate an affective and semantic context, based on previous experiences, in which to frame decisions on the beauty of visual stimuli.

Rilling and Seligman (2002) compared diverse aspects of the temporal lobes of a broad sample of primates, including humans. Their results revealed that the temporal lobe has grown in surface, volume and white matter proportion throughout human evolution. This suggests that, to a certain extent, connectivity patterns have been reorganized since the appearance of the human lineage (Schenker, et al. 2005). Rilling (2006; Rilling and Seligman 2002) has suggested that this reorganization, which is evident mainly in the left hemisphere, could be related to the appearance and expansion of regions of the temporal pole supporting linguistic functions. Specifically, the ventral visual processing stream seems to have shifted further ventrally to allow the expansion of speech and language related areas on the lateral surface of the temporal lobe, which seem to bear a close phylogenetic relation to those underlying the processing of species-specific calls in monkeys (Gil-da-Costa, et al. 2006).

In relation specifically to the temporal pole itself, there is evidence indicating that most of the functions it supports in our species are primitive. It is known that in humans this region is involved in the use of prior experiences to generate a semantic and affective context, which enhances the interpretation of the information being processed. Studies in comparative neuroanatomy have provided evidence that this region performs similar functions in other primates. Kondo and colleagues (2003) showed that the temporal pole of monkeys is richly connected to orbital and medial prefrontal cortical nets, suggesting its involvement in the integration of affective, mnemonic and sensory information. Furthermore, the results of Croxson (2005) revealed that the connectivity patterns between temporal and prefrontal cortices in humans and macaques are very similar.

Finally, it has been shown that the temporal pole plays an important role in object recognition. Lesions to this region especially impair the recognition and recall of specific entities, and familiar objects and faces (Nakamura and Kubota 1996). Experimental results support the notion that this function might constitute a homology in monkeys and humans. Vogels (1999), for instance, demonstrated that neurons in the anterior temporal cortex of monkeys are involved in the processing of visual information related to objects, and that they are sensitive to the presentation of exemplars of a learned category. Likewise, other studies reviewed by Nakamura and Kubota (1996) suggest that lesions to the monkey temporal pole can lead to deficits in the recognition of the experimenter's gloves, food or live snakes, but not in the discrimination of unfamiliar objects or patterns.

4.3. DORSOLATERAL PREFRONTAL CORTEX

The studies performed by Cela-Conde, et al. (2004) and Jacobsen, et al. (2006) revealed an increase in the lateral prefrontal cortex while partici-

pants rated the beauty of paintings, photographs and geometric designs. As mentioned above, this activity could be related to the actual decision about the beauty of visual stimuli presented in both studies.

Contrary to common assumptions about the prefrontal cortex, and specifically its lateral region, there is evidence that to a great extent its organization is functionally and cytoarchitectonically conserved in humans. Petrides and Pandya (1999) compared the connectivity patterns and cytoarchitectonic organization of the dorsolateral prefrontal cortex, which encompasses Brodmann Areas (BA) 8, 9, and 46, of macaques and humans. Their study did not reveal any new cytoarchitectonic areas in the human brain. In fact, these areas exhibited very similar features in human and macaque brains, whereby in both species the same traits could be used to distinguish the areas within this region. The degree of homology of neural architecture of this region is such that the same subdivisions of the areas can be found in both species (8Av, 8Ad, 8B, 9/46d and 9/46v). The comparative analysis of the ventrolateral prefrontal cortex of humans and macaques performed by Petrides and Pandya (2001) revealed a similar image of BA 47/12 and BA 45. The cytoarchitectonic criteria used to identify both areas in monkeys and humans were the same, as well as those used to differentiate them from dorsolateral cortex areas. Again, even the finer subdivisions of area 45 (45A and 45B) were identifiable in both species.

Although the brain organization of monkeys has been studied mainly by means of lesion studies and that of humans by means of neuroimaging studies, these two species also present functional homologies related to the lateral prefrontal cortex. As noted by Petrides (2005), the lateral cortex of humans and monkeys is functionally organized along a caudal-rostral axis and a dorsal-ventral axis. Specifically, in both species the caudal region of the prefrontal cortex (BA 8) contributes to the flexibility of attentional shifts between stimuli and the selection of responses depending on learned conditional rules. At the rostral end of this axis, the mid-dorsolateral cortex (BA 46 and BA 9/46) is involved in working memory tasks that require monitoring the selection of stimuli or the occurrence of expected events. The contribution of the mid-ventrolateral prefrontal cortex seems to be important for other executive functions, including the selection and comparison of representations of stimuli stored in short-term and long-term memory, as well as judgments based on them (Petrides 2005). Given that neuroimaging studies carried out on human participants and lesion studies on monkeys converge in their results, it seems adequate to consider that the functional and cytoarchitectonic of the human lateral cortex is a primitive trait.

However, it is true that certain aspects of the lateral prefrontal cortex distinguish humans from other primates. For instance, it is obvious that the involvement of these functions in certain human cognitive abilities,

such as language, or even aesthetic preference, does not occur in non-human primates. Second, the kind of information on which these functions are performed also seems to differ. This was demonstrated by Denys, et al. (2004), who utilized fMRI to show that activity in the prefrontal cortex while monkey and human participants viewed visual objects was much stronger in the former than in the latter. The authors interpreted this finding as evidence of the multisensory nature of the information reaching the prefrontal cortex of humans, which contrasts with the primarily visual information that reaches the prefrontal cortex of monkeys.

4.4. ANTERIOR CINGULATE CORTEX

The studies carried out by Vartanian and Goel (2004) and Jacobsen, et al. (2006) identified activity in this region while participants rated visual stimuli as beautiful or expressed high preference for them. Above, we suggested that the involvement of this brain region in aesthetic preference could be related to the awareness of the affective state induced by aesthetically pleasant stimuli. Although the anterior cingulate cortex is cytologically distinguishable from the posterior cingulate cortex in both humans and monkeys, other conspicuous differences exist. The most obvious of these is the presence of two areas in humans (BA 33 and BA 32') that are not found in other primates (Amiez, et al. 2005; Vogt, et al. 1995).

Additionally, Nimchinsky and colleagues (1999) have shown that the anterior cingulate cortex of great apes and humans contains a type of neurons, known as spindle cells that have not been found in other mammals including other primate species. In humans these neurons constitute 5.6 per cent of pyramidal cells of transverse sections of layer Vb, and appear in clusters of between 3 and 6. Among other hominoids, a similar trend is observable in bonobos. Conversely, the relative abundance of these neurons is smaller in common chimpanzees, gorillas and orangutans, and exhibits little or no clustering. These results indicate that a new kind of neuron appeared in the anterior cingulate cortex at an early point in the hominoid lineage. The abundance of these neurons gradually increased throughout evolution, and they began clustering together. Nimchinsky and colleagues (1999) hypothesized that the main function of these neurons is to integrate affective information and transmit it to motor brain regions related with vocalization, facial expression or autonomic functions. Allman and colleagues (2002) suggested that the increase in spindle cell proportion could be related to enhancements of emotional stability and self-control. Furthermore, they argued that together with the increase of the anterior frontal cortex, abundant spindle cells played a relevant role in the management of the requirements related to the growth of family size throughout human evolution.

4.5. ORBITOFRONTAL CORTEX

Kawabata and Zeki (2004) identified greater activity in the orbitofrontal cortex when their participants rated the stimuli more beautiful than when they rated them as ugly. A large number of studies have reported activity in this region when participants were delivered primary and abstract rewards, which suggests that its role in aesthetic preference could be to represent the reward value of visual stimuli.

The comparison of the orbitofrontal cortex of a considerable amount of macaques and humans revealed that the pattern of sulci and convolutions was similar in both species (Chiavaras and Petrides 2000), though the human patterns were more intricate and variable than the monkey patterns. Despite this conservation in the sulcal pattern of the orbitofrontal cortex, and other general morphological and cytological similarities, which led Semendeferi and colleagues (1998) to consider that the state of BA 13 in humans was primitive, certain features of this region distinguish humans from other apes. For instance, in humans and bonobos BA 13 is relatively smaller than in other apes. Together with other aspects, this suggests that the number of orbitofrontal cytoarchitectonic subareas has increased throughout human evolution. Additionally, the cellular density of this area in humans is the lowest among all hominoids and, together with gibbons, they have the lowest grey matter index. This means that, relatively speaking, there is a greater space occupied by axons and dendrites (Semendeferi, et al. 1998).

Rolls' (2004) revision of the functions of the orbitofrontal cortex of primates revealed that this region is functionally conserved in humans, in the sense that, as is the case with monkeys, it includes representations of smell, taste, food texture, visual information received from the ventral stream, as well as necessary information for facial recognition. In primates this information is used to identify the stimuli that are being processed and to establish their reward value. Furthermore, both in humans and monkeys the orbitofrontal cortex is a crucial element in learning associations between stimuli and rewards, and modifying them when contingencies vary.

4.6. FRONTAL POLE

Jacobsen and colleagues' (2006) results showed that while participants rated the beauty of geometric visual stimuli, activity in the frontal pole was greater than when they rated the symmetry of the same stimuli. Previous studies have found activity in this brain region during the performance of evaluative judgments of a broad range of visual materials.

Petrides and Pandya (1999) compared the macaque and human BA 10, located in the frontal pole. This study revealed that the architectonic features that distinguish this area from the surrounding ones are the same in both species. This means that the kinds of neurons in this region, as well

as their distribution in cortical layers, have varied little throughout the hominoid and human lineages.

Semendeferi and colleagues (2001) performed a qualitative and quantitative study of BA 10, comparing data taken from macaque, gibbon, orangutan, gorilla, chimpanzee, bonobo and human brains. Their results confirm that, with the exception of gorillas, BA 10 is easily identified in the frontal pole of all hominoid species. Yet, there are certain traits that distinguish BA in human beings from other hominoids. First, its size is larger, both in relative and absolute terms. Second, although humans exhibit the largest absolute amount of neurons, neural density in this region is the lowest among all hominoids. This affords a greater space for connections with cells from the same and different areas, especially, as observed by Semendeferi, et al. (2001), other association areas.

4.7. CONCLUSIONS

Our review of the comparative literature has shown that brain regions whose activity underlies aesthetic preference tasks do not share a common evolutionary pattern. In fact, the functional and cytoarchitectonic organization of some of these regions seem to have undergone little variation since the human and chimpanzee lineages split, whereas others exhibit conspicuous modifications. We believe that evolutionary approaches to aesthetic preference should be able to account for the evolutionary history of the neural correlates of such capacity. Specifically, these approaches should take into account that during the evolution of our lineage the following aspects seem to have varied little: (i) the substrates of early visual processes; (ii) the ventral visual processing stream and its involvement in the recognition and classification of objects; (iii) the cytoarchitectonic organization and connectivity of the temporal pole and its involvement in the generation of an affective and mnemonic context; (iv) the organization of the lateral, orbital and anterior prefrontal cortex, both at an anatomical and functional level. Additionally, evolutionary accounts of aesthetic preference should account for the relation between the appearance of this capacity and the following cerebral changes that occurred throughout human evolution: (i) The development of the dorsal processing stream, related to an enhanced analysis of spatial relations; (ii) the increase in the variety of sensory information reaching and processed by the prefrontal cortex; (iii) the increase in the connectivity among prefrontal cortical regions and between these and other brain regions; (iv) the appearance of novel cytoarchitectonic areas and a new kind of neurons in the anterior cingulate cortex, related to the awareness of one's own affective states.

These considerations suggest that some of the mechanisms that support the human capacity to appreciate beauty, those related to the visual representation of objects, the representation of their reward value and

certain executive functions, were already present in our primate ancestors millions of years before the emergence of our species. Our appreciation of beauty, however, also required certain brain modifications that occurred throughout human evolution, presumably related to a greater integration of sensory information, an enrichment of spatial analyses, and an enhancement of the awareness of affective states. Aesthetic preference emerged in human beings, thus, by virtue of a kind of mosaic evolution, resulting from the integration of these derived processes and structures with the pre-existing primitive ones.

5. GENERAL DISCUSSION AND CONCLUSIONS

There is a common theme running through the previous sections. Amounting evidence suggests that humans share certain cognitive mechanisms underlying language, morality and aesthetic appreciation with other primates, their closest living relatives, and even other more distantly related mammals. The principle of parsimony, which guides current comparative reasoning, suggests that, in the absence of evidence to the contrary, these cognitive mechanisms are at least as old as the common ancestor of those species. The picture of the evolution of the human mind that emerges is that of an evolutionary mosaic in which different parts of the puzzle were laid down many millions of years ago and others have very recent origins. Just as the acquisition of current bipedalism was a process that spanned millions of years and involved modifications to different parts of the skeleton at different moments throughout human evolution, language, morality, and beauty appreciation did not appear at a specific moment in time and in a given hominid species. Rather, many of the seeds for these cognitive mechanisms were present in our primate ancestors' minds. They were necessarily involved in tasks unrelated with human language, human morality and human beauty appreciation, but were later recruited for these tasks. Neuroscience has shown that the neural bases of language, morality and beauty appreciation are not absolutely specific. Especially in the last two cases, the reliance on common neural mechanisms seems to be the norm, probably reflecting the generous reliance on primitive neural and cognitive systems.

In a sense, natural selection built our cognitive uniqueness around, and taking advantage of, our primate commonalities. Hence, the current features of human language, morality, and aesthetic preference owe, to a great extent, to those ancient building blocks. On the other hand, obviously, novel cognitive features were acquired after our lineage split from chimpanzees', including the ability to master recursive grammars, linguistic duality of patterning, a sophisticated theory of mind, the awareness of

our own affective state, the enhancement of spatial processing, as well as a general increase of connectivity within and among cortical brain regions.

Thus, explanations for the evolution of these marvelous human achievements require: (i) accounting for the presence of certain components in ancestral species; (ii) accounting for the appearance of certain components along the evolution of the human lineage; and (iii) accounting for the integration of both kinds of components. However, the view of the evolution of language, morals, and aesthetic preference we have sketched, grounded on the available comparative literature, is difficult to reconcile with two of the features that characterize approaches framed within narrow evolutionary psychology, as used by Bechtel (2002) when referring to work carried out following the framework laid down by Tooby and Cosmides (1992). First, within this view, language, morality and aesthetic preference are conceived as a separate modules or cognitive programs. Second, it is assumed that evolution favored the appearance of these, and other human cognitive mechanisms, in our Pleistocene hunter-gatherer ancestors.

Evolutionary psychology in a narrow sense usually considers that language, morality and aesthetic preference constitute modules or autonomous programs, which perform a specific function to solve a specific adaptive problem faced by our ancestors living in Pleistocene environments. However, as noted by Shapiro and Epstein (1998), evolutionary approaches to human cognition do not necessarily require the adoption of this specific modular conception of the mind. They argued that it is misleading to identify cognitive processes with the tasks or objectives they are used for, as evolutionary psychologists do. Natural selection does not necessarily select different cognitive processes to resolve different adaptive problems. It is much more probable that diverse cognitive processes are involved in the solution of each of the adaptive problems pointed out by evolutionary psychologists, and that each of those processes would be useful to solve various adaptive problems. Bechtel (2002) and Atkinson and Wheeler (2004) argued that neuroscientifically sound modules do not refer to tasks such as cheater detection, mate selection, or the detection of beauty, but to finer grain sized information processing operations. These processes can be involved in a multitude of adaptively relevant tasks. With regards to language, morality and aesthetic preference, there is currently little doubt among psychologists and neuroscientists that the best way to conceive such cognitive faculties is as the result of a varied set of processes, from those related to the perception of the most basic features to those underlying deliberation and decision making.

Finally, it is usually considered that in order to explain the origin and evolution of human cognitive processes it is sufficient to understand the problems faced by our Pleistocene hunter-gatherer ancestors (Tooby and

Cosmides 1992). This assumption faces at least two main problems. First, during the Pleistocene period our ancestors lived in a variety of environments, not merely savannas (Foley 1995). In fact, the Pleistocene period saw the expansion of humans in many parts of the world, from the African plains to the woodlands of Southeast Asia and the sub-glacial valleys of northern Asia and Europe. It is difficult to see that these environments share a stable common set of selective pressures, and that these were not present, say for instance, in the environments of our Pliocene ancestors. Furthermore, the view that the origin of human cognition is to be found in Pleistocene savannas ignores that rarely in evolution do completely novel systems or mechanisms appear. This is the essence of Darwin's (1859/1991) notion of descent with modification. Just as the origin of bipedalism and human erect posture cannot be understood without reference to previous forms of locomotion and skeletal designs, human mental and neural mechanisms did not appear in a vacuum. They are surely the result of modifications to mechanisms inherited from our ancestors, including Pliocene hominids, and even earlier primates. In the words of Bechtel (2002):

[...] evolution begins with existing complex entities and modifies them. This is very different than a picture of developing new modules *de novo*. Moreover, it imposes an important constraint on evolutionary models—that they be grounded on information about phylogeny and the ancestral condition before the acquisition of a new ability (Bechtel 2002; p. 223).

There is no question that Pleistocene environments exerted strong selective pressures on our ancestors in relation to language, morality and the appreciation of beauty, among many other cognitive and physical traits. The literature provides evidence of changes in cognitive and neural systems throughout this period of human evolution. But the fact is that these pressures were acting on brain structures and processes that had been inherited from earlier ancestors. Our review of the literature has shown that part of the cognitive and neural underpinnings of language, morality, and aesthetic preference were already in place millions of years ago in our primate ancestors, which we share with some current primate species. Hence, evolutionary approaches to the human mind cannot limit the study of the selective pressures and environments to those affecting our savanna dwelling hunter-gatherer ancestors. We believe that knowledge of the selective pressures acting on early hominids, hominoids, and maybe even earlier primates, as well as their cognitive adaptations, will provide a rich and necessary complement to understanding the evolution of the cognitive traits that have traditionally been regarded as defining our humanity.

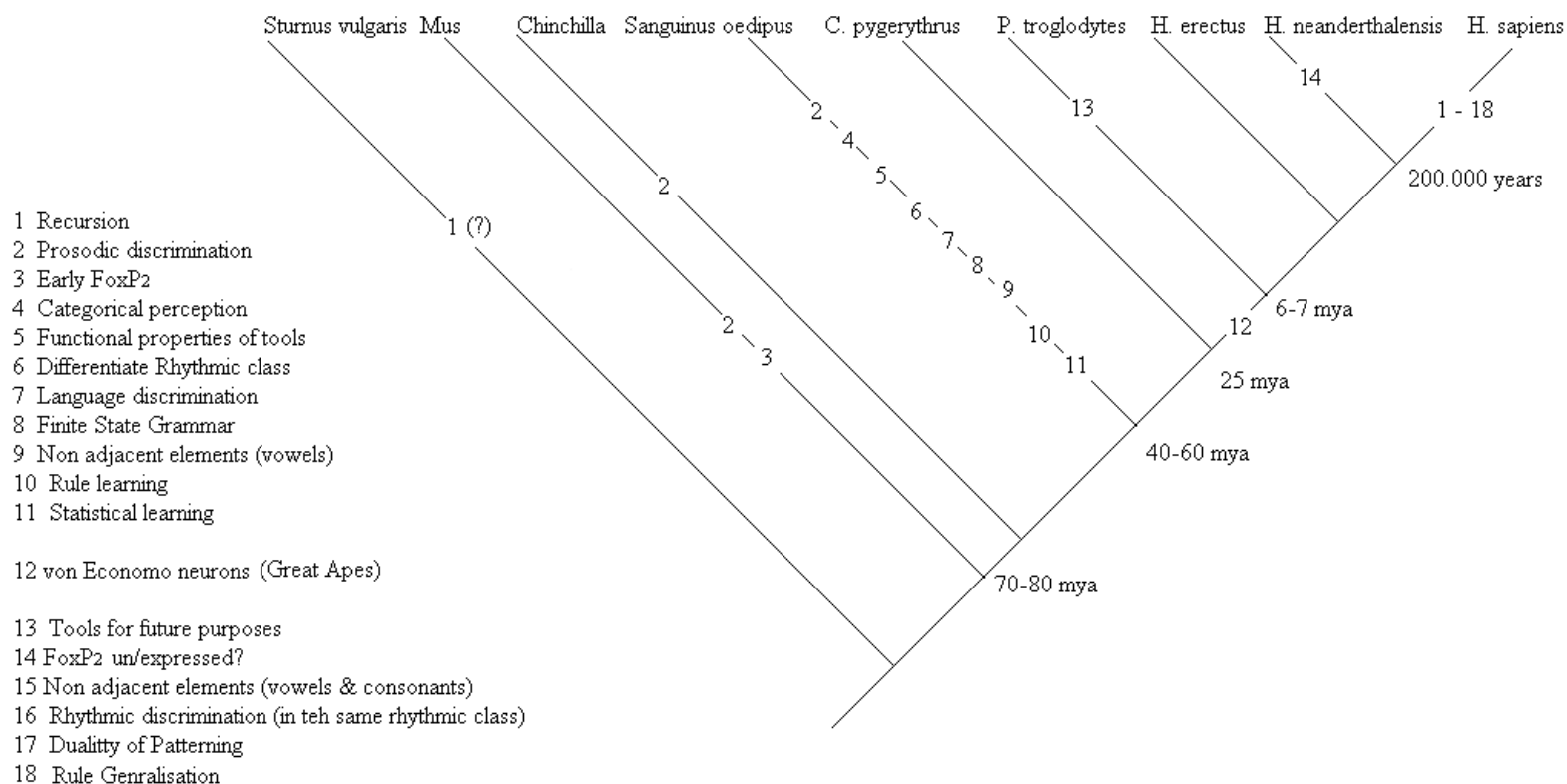


FIGURE 1
 A cladogram representing at which state can be assigned the linguistic micro-abilities and some physiological traits. This represents the until now attested data in extant and extinct species different from *H. sapiens*.
 Note the lack of information in some clades, in contrast with the *S. oedipus* clade.

This research was made possible by project research grant HUM2007-64086/FISO awarded by the *Dirección General de Investigación del Ministerio de Educación y Ciencia*.

REFERENCES

- Allman, J., Hakeem, A. and Watson, K. (2002), "Two phylogenetic specializations in the human brain," *The Neuroscientist* 8: 335-346.
- Amiez, C., Joseph, J.-P. and Procyk, E. (2005), "Primate anterior cingulate cortex and adaptation of behavior," in S. Dehaene, J.-R. Duhamel, M. D. Hauser and G. Rizzolatti (eds.), *From Monkey Brain to Human Brain* (pp. 315-336). Cambridge, MA: MIT Press.
- Atkinson, A. P. and Wheeler, M. (2004), "The grain of domains: the evolutionary-psychological case against domain-general cognition," *Mind and Language* 19: 147-176.
- Barton, R. A. (2006), "Primate brain evolution: Integrating comparative, neurophysiological, and ethological data," *Evolutionary Anthropology* 15: 224-236.
- Bechtel, W. (2002), "Modules, brain parts, and evolutionary psychology," in S. J. Scher and F. Rauscher (eds.), *Evolutionary Psychology: Alternative Approaches* (pp. 211-227). Dordrecht: Kluwer.
- Bekoff, M. (2002a), "Empathy: Common sense, science sense, wolves and well-being. Commentary on Preston and de Waal: 'Empathy: Its ultimate and proximate bases'," *Behavioral and Brain Sciences* 25: 26-27.
- Bekoff, M. (2002b), *Minding Animals: Awareness, Emotions and Heart*. Oxford: Oxford University Press.
- Brosnan, S. F. and de Waal, F. B. M. (2003), "Monkeys reject unequal pay," *Nature* 425: 297-299.
- Brown, J. L. (1983), "Cooperation — a biologist's dilemma," in J. S. Rosenblatt (ed.), *Advances in the Study of Behavior*. London: Academic Press, pp 1-37.
- Byrne, R. W. and Whiten, A. (1988), *Machiavellian Intelligence: Social Expertise and the Evolution of Intellect in Monkeys, Apes, and Humans*, New York: Oxford University Press.
- Call, J. (2005), "Descartes' two errors: Reason and reflection in the great apes," in S. Hurley and M. Nudds (Eds.), *Rational Animals* (pp. 219-234). Oxford: Oxford University Press.
- Call, J. and Tomasello, M. (1998), "Distinguishing intentional from accidental actions in orangutans (*Pongo pygmaeus*), chimpanzees (*Pan troglodytes*), and human children (*Homo sapiens*)," *Journal of Comparative Psychology* 112: 192-206.
- Call, J. and Tomasello, M. (2008), "Does the chimpanzee have a theory of mind? 30 years later," *Trends in Cognitive Sciences* 12: 187-192.
- Call, J., Hare, B., Carpenter, M. and Tomasello, M. (2004), "'Unwilling' versus 'unable': chimpanzees' understanding of human intentional action," *Developmental Science* 7: 488-498.
- Cela-Conde, C. J., Marty, G., Maestú, F., Ortiz, T., Munar, E., Fernández, A., Roca, M., Rosselló, J. and Quesney, F. (2004), "Activation of the prefrontal cortex in the human visual aesthetic perception," *Proceedings of the National Academy of Sciences USA* 101: 6321-6325.

- Chatterjee, A. (2003), "Prospects for a cognitive neuroscience of visual aesthetics," *Bulletin of Psychology of the Arts* 4: 55-60.
- Chiavaras, M. M. and Petrides, M. (2000), "Orbitofrontal sulci of the human and macaque monkey brain", *The Journal of Comparative Neurology* 422: 35-54.
- Corballis, M. C. (2002), *From Hand to Mouth: The Origins of Language*. Princeton University Press.
- Cords, M., Aureli, F. (2000), "Reconciliation and relationship qualities," in F. Aureli, de Waal, F.B.M. (ed.), *Natural Conflict Resolution* (pp. 177-198). California: University of California Press.
- Croxson, P. L., Johansen-Berg, H., Behrens, T. E. J., Robson, M. D., Pinski, M. A., Gross, C. G., Richter, W., Richter, M. C., Kastner, S. and Rushworth, M. F. S. (2005), "Quantitative investigation of connections of the prefrontal cortex in the human and macaque using probabilistic diffusion tractography," *The Journal of Neuroscience* 25: 8854-8866.
- Darwin, C. (1859/1991), *The Origin of Species*. Amherst NY: Prometheus Books.
- Darwin, C. (1871), *The Descent of Man, and Selection in Relation to Sex*. London: John Murray.
- de Waal, F. (1982), *Chimpanzee Politics: Power and Sex among Apes*. London: Jonathon Cape.
- de Waal, F. (1997), "The chimpanzee's service economy: Food for grooming," *Evolution and Human Behavior* 18: 375-386.
- de Waal, F. (2003), "Morality and the social instincts: continuity with other primates," in *The Tanner Lectures on Human Values*. Princeton: Princeton University Press.
- de Waal, F. (2007), "Putting altruism back into altruism: The evolution of empathy," *Annual Review of Psychology* 59: 279-300.
- de Waal, F. and Aureli, F. (1996), "Consolation, reconciliation, and a possible cognitive difference between macaques and chimpanzees," in A. E. Russon, Bard, K.A., Taylor, S. (eds.), *Reaching Into Thought: The Minds of the Great Apes* (pp. 80-110). New York, NY: Cambridge University Press.
- de Waal, F. and Berger, M. (2000), "Payment for labour in monkeys," *Nature* 404: 563.
- de Waal, F. and Lanting, F. (1998), *Bonobo. The Forgotten Ape*. California: University of California Press.
- Denys, K., Vanduffel, W., Fize, D., Nelissen, K., Sawamura, H., Georgieva, S., Vogels, R., Van Essen, D. and Orban, G. A. (2004), "Visual activation in prefrontal cortex is stronger in monkeys than in humans," *Journal of Cognitive Neuroscience* 16: 1505-1516.
- Edwards, S., Snowdon, C. (1980), "Social behavior of captive, group-living orangutans," *International Journal of Primatology* 1: 39-62.
- Fitch, W. T. and Hauser, M. D. (2004), "Computational constraints on syntactic processing in a non-human primate," *Science* 30: 377-380.
- Flack, J. C. and de Waal, F. B. M. (2000), "'Any animal whatever' — Darwinian building blocks of morality in monkeys and apes," *Journal of Consciousness Studies* 7: 1-29.
- Foley, R. (1995), "The adaptive legacy of human evolution: a search for the environment of evolutionary adaptedness," *Evolutionary Anthropology* 4: 194-203.
- Gallistel, C. R. and Cramer, A. E. (1996), "Computations on metric maps in mammals: getting oriented and choosing a multi-destination route," *The Journal of Experimental Biology* 199: 211-217.

- Gentner, T. Q., Fenn, K. M., Margoliash, D. and Nusbaum, H. C. (2006), "Recursive syntactic pattern learning by songbirds," *Nature* 440: 1204-1207.
- Gil-da-Costa, R., Martin, A., Lopes, M. A., Muñoz, M., Fritz, J. B. and Braun, A. R. (2006), "Species-specific calls activate homologs of Broca's and Wernicke's areas in the macaque," *Nature Neuroscience* 9: 1064-70.
- Gomez, J. C. (2005), "Species comparative studies and cognitive development," *Trends in Cognitive Sciences* 9: 118-125.
- Gómez, J. C. (2007). *El desarrollo de la mente en los simios, los monos y los niños*. Madrid: Morata.
- Hare, B., Call, J. and Tomasello, M. (2001), "Do chimpanzees know what conspecifics know and do not know?" *Animal Behaviour* 61: 139-151.
- Hauser, M. D. (2001), *Wild Minds: What Animals Really Think*. New York, NY: Henry Holt/Penguin, UK.
- Hauser, M. D., Chen, M. K., Chen, F. and Chuang, E. (2003), "Give unto others: genetically unrelated cotton-top tamarin monkeys preferentially give food to those who altruistically give food back," *Proceedings of the Royal Society of London Series B-Biological Sciences* 270: 2363-2370.
- Hauser, M. D., Chomsky, N. and Fitch, W. T. (2002), "The faculty of language: what is it, who has it, and how did it evolve?" *Science* 298: 1569-1579.
- Hauser, M. D., Newport, E. L. and Aslin, R. N. (2001), "Segmentation of the speech stream in a non-human primate: statistical learning in cotton-top tamarins," *Cognition* 78: B53-64.
- Hauser, M. D., Weiss, D. and Marcus, G. (2002), "Rule learning by cotton-top tamarins," *Cognition* 86: B15-22.
- Heyes, C. M. (1998), "Theory of mind in non-human primates," *Behavioral and Brain Sciences* 21: 101-148.
- Hockett, C. F. (1960), "The origin of speech," *Scientific American* 203: 89-96.
- Jacobsen, T., Schubotz, R. I., Höfel, L. and von Cramon, D. Y. (2006), "Brain correlates of aesthetic judgment of beauty," *Neuroimage* 29: 276-285.
- Kaminski, J., Call, J. and Fischer, J. (2004), "Word learning in a domestic dog: evidence for 'fast mapping'," *Science* 304: 1682-1683.
- Kaminski, J., Fischer, J. and Call, J. (2008), "Prospective object search in dogs: mixed evidence for knowledge of what and where," *Animal Cognition* 11: 367-371.
- Kawabata, H. and Zeki, S. (2004), "Neural correlates of beauty," *Journal of Neurophysiology* 91: 1699-1705.
- Kondo, H., Saleem, K. S. and Price, J. L. (2003), "Differential connections of the temporal pole with the orbital and medial prefrontal networks in macaque monkeys," *The Journal of Comparative Neurology* 465: 499-523.
- Kuhl, P. K. and Miller, J. D. (1975), "Speech perception by the chinchilla: voiced-voiceless distinction in alveolar plosive consonants," *Science* 190: 69-72.
- Manson, J. H., Perry, S. and Stahl, D. (2005), "Reconciliation in wild white-faced capuchins (*Cebus capucinus*)," *American Journal of Primatology* 65: 205-219.
- Marcus, G. F. (2006), "Language: startling starlings," *Nature* 440: 1117-1118.
- Marcus, G. F., Vijayan, S., Bandi Rao, S. and Vishton, P. M. (1999), "Rule learning by seven-month-old infants," *Science* 283: 77-80.
- Munakata, Y., Santos, L. S., Spelke, E. S., Hauser, M. D. and O'Reilly, R. C. (2001), "Visual representation in the wild: How rhesus monkeys parse objects," *Journal of Cognitive Neuroscience* 13: 44-58.
- Nakamura, K. and Kubota, K. (1996), "The primate temporal pole: its putative role in object recognition and memory," *Behavioural Brain Research* 77: 53-77.

- Nazzi T., Jusczyk P.W. and Johnson E.K. (2000), "Language Discrimination by English-Learning 5-Month-Olds: Effects of Rhythm and Familiarity," *Journal of Memory and Language* 43: 1-19.
- Newport, E. L., Hauser, M. D., Spaepen, G. and Aslin, R. N. (2004), "Learning at a distance II. Statistical learning of non-adjacent dependencies in a non-human primate," *Cognitive Psychology* 49: 85-117.
- Nichols, S. and Mallon, R. (2006), "Moral dilemmas and moral rules," *Cognition* 100: 530-542.
- Nimchinsky, E. A., Gilissen, E., Allman, J. M., Perl, D. L., Erwin, J. M. and Hof, P. R. (1999), "A neuronal morphologic type unique to humans and great apes," *Proceedings of the National Academy of Sciences USA* 96: 5268-5273.
- Okanoya, K. (2007), "Language evolution and an emergent property," *Current Opinion in Neurobiology* 17: 271-276.
- Orban, G. A., Van Essen, D. and Vanduffel, W. (2004), "Comparative mapping of higher visual areas in monkeys and humans," *Trends in Cognitive Sciences* 8: 315-324.
- Petrides, M. (2005), "Lateral prefrontal cortex: architectonic and functional organization," *Philosophical Transactions of the Royal Society B* 360: 781-795.
- Petrides, M. and Pandya, D. N. (1999), "Dorsolateral prefrontal cortex: comparative cytoarchitectonic analysis in the human and macaque brain and cortico-cortical connection patterns," *European Journal of Neuroscience* 11: 1011-1036.
- Petrides, M. and Pandya, D. N. (2001), "Comparative cytoarchitectonic analysis of the human and the macaque ventrolateral prefrontal cortex and cortico-cortical connection patterns in the monkey," *European Journal of Neuroscience* 16: 291-310.
- Pinker, S. (1994), *The Language Instinct. How the Mind Creates Language*. New York: William Morrow.
- Povinelli, D. J. and Vonk, J. (2003), "Chimpanzee minds: suspiciously human?" *Trends in Cognitive Sciences* 7: 157-160.
- Preston, S. D. and de Waal, F. (2002), "Empathy: Its ultimate and proximate bases," *Behavioral and Brain Sciences* 25: 1-72.
- Preuss, T. M. and Coleman, G. Q. (2002), "Human-specific organization of primary visual cortex: Alternating compartments of dense Cat-301 and Calbindin immunoreactivity in layer 4A," *Cerebral Cortex* 12: 671-691.
- Reiss, D. and Marino, L. (2001), "Mirror self-recognition in the bottlenose dolphin: A case of cognitive convergence," *Proceedings of the National Academy of Sciences of the United States of America* 98: 5937-5942.
- Rilling, J. K. (2006), "Human and nonhuman primate brains: Are they allometrically scaled versions of the same design?" *Evolutionary Anthropology* 25: 65-77.
- Rilling, J. K. and Seligman, R. A. (2002), "A quantitative morphometric comparative analysis of the primate temporal lobe," *Journal of Human Evolution* 42: 505-533.
- Rolls, E. T. (2004), "Convergence of sensory systems in the orbitofrontal cortex in primates and brain design for emotion," *The Anatomical Record Part A*, 281A: 1212-1225.
- Rose, L. M. (1997), "Vertebrate predation and food-sharing in Cebus and Pan," *International Journal of Primatology* 18: 727-765.
- Roselló, Joana. (2006), "Combinatorial properties at the roots of language: Duality of patterning and recursion," in Roselló, Joana and Martín, Jesús (eds.), *The Biolinguistic Turn. Issues on Language and Biology* (p. 278). Barcelona: PPU, S.A.

- Sasaki, Y., Vanduffel, W., Knutsen, T., Tyler, C. and Tootell, R. (2005), "Symmetry activates extrastriate visual cortex in human and nonhuman primates," *Proceedings of the National Academy of Sciences USA* 102: 3159-3163.
- Schenker, N. M., Desgouttes, A.-M. and Semendeferi, K. (2005), "Neural connectivity and cortical substrates of cognition in hominoids," *Journal of Human Evolution* 49: 547-569.
- Schoenemann, P. T. (2006), "Evolution of the size and functional areas of the human brain," *Annual Review of Anthropology* 35: 379-406.
- Semendeferi, K., Armstrong, E., Schleicher, A., Zilles, K. and Van Hoesen, G. W. (1998), "Limbic frontal cortex in hominoids: A comparative study of area 13," *American Journal of Physical Anthropology* 106: 129-155.
- Semendeferi, K., Armstrong, E., Schleicher, A., Zilles, K. and Van Hoesen, G. W. (2001), "Prefrontal cortex in humans and apes: A comparative study of area 10," *American Journal of Physical Anthropology* 114: 224-241.
- Shapiro, L. and Epstein, W. (1998), "Evolutionary theory meets cognitive psychology: a more selective perspective," *Mind and Language* 13: 171-194.
- Sigala, N., Gabbiani, F. and Logothetis, N. K. (2002), "Visual categorization and object representation in monkeys and humans," *Journal of Cognitive Neuroscience* 14: 187-198.
- Stevens, J. R. and Hauser, M. D. (2004), "Why be nice? Psychological constraints on the evolution of cooperation," *Trends in Cognitive Sciences* 8: 60-65.
- Tincoff, R., Hauser, M., Tsao, F., Spaepen, G., Ramus, F. and Mehler, J. (2005), "The role of speech rhythm in language discrimination: further tests with a non-human primate," *Developmental Science* 8: 26-35.
- Tomasello, M., Call, J. and Hare, B. (2003a), "Chimpanzees understand psychological states—the question is which ones and to what extent," *Trends in Cognitive Sciences* 7: 153-156.
- Tomasello, M., Call, J. and Hare, B. (2003c), "Chimpanzees versus humans: It's not that simple," *Trends in Cognitive Sciences* 7(6): 239-240.
- Tooby, J. and Cosmides, L. (1992), "The psychological foundations of culture," in J. H. Barkow, L. Cosmides and J. Tooby (Eds.), *The Adapted Mind*. New York, NY: Oxford University Press.
- Toro, J. M., Trobalon, J. B. and Sebastián-Gallés, N. (2003), "The use of prosodic cues in language discrimination tasks by rats," *Animal Cognition* 6(2): 131-6.
- Trivers, R. L. (1971), "Evolution of reciprocal altruism," *Quarterly Review of Biology* 46: 35-57.
- van Wolkenten, M., Brosnan, S. F. and De Waal, F. B. M. (2007), "Inequity responses of monkeys modified by effort," *Proceedings of the National Academy of Sciences of the United States of America* 104: 18854-18859.
- Vartanian, O. and Goel, V. (2004), "Neuroanatomical correlates of aesthetic preference for paintings," *Neuroreport* 15: 893-897.
- Vogels, R. (1999), "Categorization of complex visual images by rhesus monkeys. Part 2: single-cell study," *European Journal of Neuroscience*, 11: 1239-1255.
- Vogt, B. A., Nimchinsky, N. A., Vogt, L. J. and Hof, P. R. (1995), "Human cingulate cortex: Surface features, flat maps, and cytoarchitecture," *The Journal of Comparative Neurology*, 359: 490-506.