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From: József Topál, Ádám Miklósi, Márta Gácsi, Antal Dóka, Péter Pongrácz, Enikő Kubinyi, Zsófia Virányi, and Vilmos Csányi, The Dog as a Model for Understanding Human Social Behavior. In H. Jane Brockmann, Timothy J. Roper, Marc Naguib, Katherine E. Wynne-Edwards, John C. Mitani, Leigh W. Simmons, editors: *Advances in The Study of Behavior*, Vol. 39, Burlington: Academic Press, 2009, pp. 71-116.

ISBN: 978-0-12-374474-6 © Copyright 2009 Elsevier Inc.

Academic Press.

The Dog as a Model for Understanding Human Social Behavior

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I. INTRODUCTION

One of the important and controversial questions for cognitive science is “What makes human behavior and cognition unique in the animal kingdom?” From an empirical viewpoint, not denying the widely accepted premise that the evolution of human behavior rests crucially on uniquely human abilities, this question could be raised either from an evolutionary or from a developmental perspective. While the first approach focuses on the question, “What kind of specific changes took place during hominization?,” the second approach points to the role of human social environment in the emergence of human behavior.

In searching for answers to these questions, different disciplines argue for different approaches suggesting theoretical and/or experimental analyses of human behavioral evolution and its underlying cognitive processes. At present, comparative social cognition is widely believed to be the most relevant discipline to deepen our understanding of the evolutionary origins of human behavior. Comparative social cognition looks for the presence or absence of human-like skills in animals that are often directly comparable at the behavioral level and suggests that the issue of human uniqueness can be addressed by asking about the specific behaviors of our species with respect to cognitive functioning.

The empirical answer to this question is, however, complex because behavioral traits and their underlying cognitive mechanisms develop as a result of epigenetic processes consisting of interactions between the social

and nonsocial environment and the genetic makeup of the organism. According to the traditional ethological approach (Tinbergen, 1963), we must first understand the function of a behavioral trait before speculating about its underlying cognitive processing, that is, one must first separate functionally distinctive components of the observable behavioral “phenotype.”

One widely used paradigm is the comparative analysis of human and nonhuman primate behavior, aimed at tracing the evolutionary origins of uniquely human skills (e.g., Povinelli et al., 1999; Tomasello and Call, 1997). This paradigm utilizes the homologous evolutionary relationship between extant nonhuman primates and humans who shared a common ancestor at some time in the distant past. Such comparative research programs are centered around the problem of whether the origin of some behavioral traits or cognitive skills can be traced back in time, that is, whether they can be assumed to have been present in the common ancestor or, alternatively, whether they have evolved after the “split” and thus are possibly adaptive (see Gould and Vbra, 1982) human-specific traits in *Homo sapiens*.

Comparative work, for example, has revealed an array of social behavioral traits which appear to have a common origin in *Homo* and apes (e.g., de Waal, 1996). The differences between humans and nonhuman great apes are of great importance because they call for specific hypotheses about the selective nature of ecological and social environments that provided the evolutionary scenario(s) since our lineage split from the other great apes (Hermann et al., 2007).

However, chimpanzees and humans not only are separated by 6 million years of evolution but they also occupy and are adapted to different niches. Species specific ecological niches can be characterized by different levels of social complexity and involve different “social problems” to solve (Humphrey, 1976). In principle, therefore, any of the social-cognitive abilities of these species could have been formed by specific adaptational demands. These selective forces were either shared for the two species (i.e., acted before the split of Pan-Homo lineage), or were different (i.e., emerged after the Pan-Homo split).

It seems that many of the specific features of human social cognition have emerged after the pan-Homo split, and therefore, we cannot explore these by the traditional human–ape comparisons. Accordingly, novel approaches may contribute a lot to exploring the evolutionary origins of the uniquely complex human cognition and behavior.

II. THE HUMAN BEHAVIOR COMPLEX

During evolution, humans adopted a set of species-specific skills that influenced critically their social life, allowing them, for example, to form large, closed individual groups (Csányi, 2001). These include advanced cognitive skills as well as other behavioral traits which have evidently played a role in the manifestation of human-specific cognitive skills. It is unlikely that the separate effect of a single or a few behavioral features determined human evolution (see, e.g., Csányi, 2000 arguing against this approach). Most probably a wide horizon of social behaviors changed in parallel, and had a joint and synergistic effect of behavioral changes. The assembly of these traits is referred to as the “Human Behavior Complex” (Csányi, 2000).

According to Csányi (2000), during human evolution social behavior has changed in three important aspects: sociality, synchronization, and constructive activity. These can be used as broad collective groups of social behavior traits.

A. SOCIALITY

The first one refers to those components of social behavior that contributed to marked changes in sociality. After socialization, individuals in human groups express strong attachment to each other (Bowlby, 1972). At the group level, this is manifested as loyalty, and presents a sharp contrast to the agonistic attitudes toward strange groups (xenophobia; LeVine and Campbell, 1973). Decreased aggressive tendencies and increased self-control facilitate the emergence of complex cooperative interactions, which are characterized by the subdivision of joint tasks into a set of complementary actions (Reynolds, 1993). Switching the role of the initiator in executing collaborative activities seems to be a unique feature of our species. Finally, humans have the ability to form groups that have their own identity (Csányi, 2001).

B. SYNCHRONIZATION

Synchronizing activities have a facilitating effect on the interaction of group members. Such synchronization is achieved by the employment of different means, such as the ability for emotional contagion (Hatfield et al., 1993), empathy or reliance on rhythms, dance and music. In addition, synchronization can be also increased by behavioral mimicry (“blind” imitation), and activities involving teaching (Csibra and Gergely, 2006)

and other disciplining behaviors. The spontaneous human tendency to follow social rules (de Waal, 1996) is especially advantageous in organizing the behavior of humans living in large groups. It is assumed that through a process of internalization, social rules are incorporated in the representational system of dominance–submission relationships, and consequently humans possess a hybrid rank order system consisting of relative rankings of both individuals and particular social rules. This trait paved the way for the emergence of complex and variable social structures in human communities. At the same time, individuals are often members of different groups, follow different rules, and live in parallel and divergent rank orders. Moreover, humans in general are able to extract social rules by experiencing and observing actions and the interactions of others, similar to how a child extracts the rules of language when overhearing linguistic interactions.

C. CONSTRUCTIVE ACTIVITY

The third group of traits is concerned with the constructive character of social behavior. In contrast to animal communication systems that transmit mainly the inner motivational state of the signaler, human language enables the transfer of complex mental representations involving past, present, and future states, such as plans and desires. Being an open system, it is in principle suited for transmitting an infinite number of messages. The language system is able to represent actors, actions, and phenomena as events occurring in the environment. In addition they can be combined into novel representations as a reconstruction of reality (Brown, 1973). Importantly, such categorical representations do not presuppose the presence of language, and are very likely present in many nonhuman species (Bickerton, 1990).

Humans are not exceptional among animals in using tools, although nonhuman tool use is highly restricted for solving special tasks. Human tool use can be considered as an open constructive system that is isomorphic with linguistic competence and conceptual thinking. Humans can construct novel objects based on planning, can combine different tools, and can use them to make further tools. Objects are integrated parts of social interactions and their use and construction is heavily dependent on and influenced by, social rules, enabling the creation of machines and technologies.

The closed social system based on increased sociality together with synchronization, constructing, and conceptual abilities, has provided the basis for rich variation in individual action plans. This in turn has resulted in rapid cultural evolution. Most of the activities of these closed groups are directed upon themselves; so as a result, the group continuously reconstructs itself over time (Csányi, 1989).

The decomposition of the Human Behavior Complex into traits that can be investigated separately (see relevant parts of [Table 1](#)), offers a descriptive framework for making behavioral comparisons between human and nonhuman species. The value of this comparative model depends on the degree to which the tallies of this complex can be experimentally tested and evaluated in the animal species under study.

III. COMPARATIVE APPROACHES FOR THE UNDERSTANDING OF HUMAN UNIQUENESS

Having been summarized those features of human social behavior that are assumed to have undergone marked changes after the *Pan-Homo* split, in the following sections of this review we point to the limitations of human–ape comparisons and provide arguments for developing convergent models. We propose that domestic dog (*Canis familiaris*) is a promising candidate for convergent modeling as this species not only illustrates a single aspect of human behavior but there is a complex level of similarity in a set of functionally shared behavioral features.

Then we offer a step-by-step procedure on how to identify and utilize functionally analogous behaviors between dogs and humans and we apply the proposed approach to the case of dog–human attachment.

Finally, we summarize experimental evidence showing behavioral parallels between dogs and humans and define Dog Behavior Complex as a set of components that makes the dog compatible with human social environment.

A. LIMITATIONS OF HUMAN–APE COMPARISONS

In spite of the indisputable advantages for using homolog models in scientific investigations, human–ape comparisons also have clear limitations. Although the homologue model has a natural appeal to most scientists, recent reviews suggest that this approach is constrained both from theoretical and practical points of view ([Boesch, 2007](#)). Space constraints allow us to discuss only three of the most important constraints.

1. *Problems in Verifying the Key Factor of the Evolution of Human Uniqueness*

While searching for the “crucial difference” between human and nonhuman behavior and the underlying cognitive mechanisms, many researchers have focused on a single causal chain of events involving the effect of

TABLE I
A FUNCTIONAL COMPARISON OF THE HUMAN BEHAVIOR COMPLEX AND THE DOG BEHAVIOR COMPLEX

Category/dimension	Distinctive and shared components of social behavior	
	Human ^a	Dog-human mixed groups
Sociality	Attachment Food sharing and inequity avoidance Group loyalty Group individuality Duality of intraspecific aggression <ul style="list-style-type: none"> ● Low level of intragroup aggression ● High level of intergroup aggression 	Attachment to humans (Gácsi et al., 2001; Nagasawa et al., 2009; Palmer and Custance, 2008; Prato-Provido et al., 2003; Topál et al., 1998, 2005a) Inequity avoidance (Range et al., 2009) Low level of intragroup aggression (Gácsi et al., 2005)
Synchronization	Emotional synchronization Behavioral synchronization <ul style="list-style-type: none"> ● Social learning ● Rule following ● Complementary cooperation ● Ritual behavior ● Pedagogical receptivity ● Selective imitation ● Teaching 	Emotional synchronization (Odendaal and Meintjes, 2003) Social learning (McKinley and Young, 2003; Pongrácz et al., 2001a,b, 2003a,b; Topál et al., 2006a) Obeying behavioral rules (Kubinyi et al., 2003a; Topál et al., 2005b) Complementary cooperation (Naderi et al., 2001) Pedagogical receptivity: “blind” replication of the human’s behavior (Erdőhegyi et al., 2007; Szeteci et al., 2003) Selective imitation (Range et al., 2007)

Constructive activity

Constructing communication

- Recognizing communicative intent of others
- Initializing communication
- Comprehension of the referential character of the gestures
- Linguistic skills

Selective responsiveness to human attention ([Call et al., 2003](#); [Gácsi et al., 2004](#); [Schwab and Huber, 2006](#); [Virányi et al., 2004](#))

Pointing behavior ([Miklósi et al. 2000](#)), initializing eye contact ([Miklósi et al., 2003](#))

Utilizing human directional gestures ([Miklósi et al., 1998](#); [Riedel et al., 2008](#); [Soproni et al., 2002](#))

Linguistic skills: fast mapping, learning by exclusion ([Kaminski et al., 2004](#)), using lexigrams to communicate requests ([Rossi and Ades, 2008](#))

Tool use

Tool construction

The former consists of important behavioral traits (components) that are assumed to have played an important role in Hominine evolution (only the main components are listed; modified after [Csányi, 2000](#)). In the case of the later, we provide a list of functionally convergent behavioral features that have gained some experimental support in recent research.

“For detailed references in the case of the Human Behavior Complex see [Csányi, 2000](#).”

environmental factors and adaptive behavioral responses or they have argued for a restricted set of cognitive skills gaining significance during our evolution.

In line with this approach, several theorists have developed specific proposals about human uniqueness. Tomasello et al. (1993), for example, pointed out the importance of complementary cognitive mechanisms (e.g., linguistic skills, theory of mind) that make someone able to learn “culturally.” In a more recent study, Tomasello et al. (2005) have argued that the crucial difference between human and nonhuman cognition is in the ability of “shared intentionality” based on construction of dialogic cognitive representations and mind reading. Other key features of hominization are supposed to be the emergence of identification-based imitative learning (Tomasello et al., 2003), or the evolution of the ability to teach and to learn from teaching (pedagogical receptivity—Csibra and Gergely, 2006). Regarding the human specificity of imitative abilities it has been shown, for example, that humans but not chimpanzees tend to copy even when it is not obvious how the action will bring about a desired result (Horner and Whiten, 2005).

Others suggest that as a result of hominization the importance of direct aggression in the maintenance of partnership and rank order within the group has gradually diminished, while within group interactions have been increasingly influenced by cooperative tendencies (Hare and Tomasello, 2005). These specific changes in temperament might have freed socio-cognitive abilities from situational limitations in humans. For example, visual perspective taking is a highly generalizable skill among humans and has especial importance in the development of understanding communicative referential acts in infants (e.g., Flom et al., 2004). Chimpanzees, however, show this ability only when competing for food and not in cooperative tasks (Hare et al., 2000; Povinelli et al., 1990). The fact that apes usually underperform in cooperative tasks suggests that their social competence is biased toward competitive situations (Hare, 2001). In line with this assumption recent experiments seem to provide evidence that apes (Melis et al., 2006), unlike humans (Warneken and Tomasello, 2007), show limitations in cooperation.

The general problem with such ideas is that due to a lack of historical data there are problems in verifying the evolutionary scenario. Also, the emphasis on a single “main” cognitive feature obscures the real complexity of sociocognitive behavior. Such sequential approaches to human behavioral evolution can be contrasted with system theoretical models (Csányi, 1989) emphasizing the parallel nature of changes that have taken place in the process of human behavioral evolution. Accordingly, parallel emergence of some behavioral alterations and their simultaneous presence might provide a more plausible hypothesis for human-specific behavior.

In line with these, human evolution is best viewed as a process that affected many features of social behavior in a complex interacting way (Byrne, 2005; Hermann et al., 2007).

2. *Concerns with the Sample Size, Rearing Condition, and Differences in Social Experience*

In contrast to the large number of human subjects who have been involved in experimental studies of social-cognitive abilities, most nonhuman ape studies were conducted on a few human-reared subjects. The traditional technique has been to bring wild-caught animals to the laboratory and/or socialize captive born individuals with humans. However, this has introduced a complicating factor because these apes or monkeys are variously constrained in getting species-specific experience and, in addition, they are exposed to a variable extent to some aspects of the human social environment. Therefore, behavioral resemblances or similarities in performance could often be dismissed as peculiarities of the subjects' exposure to humans, while any differences could be explained by the lack of either familiarization with the human environment and/or social behavior or the lack of species-specific experiences (e.g., Bering, 2004). The high variability in environmental experience and the low number of individuals studied raise problems of external validity including the reproducibility of the research. This is most striking when a few "arbitrarily chosen" apes are compared to a large number of children. What is more, adult apes are often compared to human infants without controlling for external variables including previous experience and experimental/developmental factors.

3. *Welfare Problems*

The maintenance of apes and monkeys in captivity for experimental purposes creates an unsolvable welfare problem because these artificial environments cannot fulfill the natural needs of the species. The paradox here is that the more we know about the apes' complex social and mental skills, the less we become entitled to keep them under artificial conditions. Even if there are possibilities that could offer partial solution for the problems raised above (e.g., studying apes at habituated sites in their natural environment; Boesch et al., 1994), it is time to look for alternative and complementary paradigms.

B. CONVERGENT MODELING

While the evolutionary reasoning behind homologue models seems to be simple and straight forward, the argument for developing convergent models is more complicated. Convergent evolution is assumed when similarities

between evolutionarily unrelated characters of species are attributed to their independent adaptation to similar environments. Thus, the detection of phenotypic convergence in different species lies at the heart of the evolutionary argument because it provides critical evidence for the operation of adaptive processes. However, adaptation is a complex process that may involve single traits, correlated traits, or even a set of complex changes (Gould and Vbra, 1982). For example, to adapt to living in water, Cetaceans underwent a series of changes including morphological (e.g., skin, limbs, and body form), physiological (e.g., brain functioning, breath regulation), and behavioral (e.g., communication) modifications (see also Marino, 2002).

From our point of view, the most interesting question is whether such changes are single isolated convergent adaptations or whether they should be viewed as a complex set of traits emerging in concert. This is particularly important in the case of human evolution where one tries to separate homologous traits from those that emerged under neutral conditions or are adaptations to certain environmental challenges. In the case of behavior, the only possible solution seems to be to look for other organisms that evolved under similar adaptational challenges. Studies on a wide range of species seem to suggest that convergent approaches would be useful (e.g., dolphins: Herman, 2002; corvids: Emery and Clayton, 2001), but these are functionally restricted in the sense that they model only a narrow aspect of human behavior.

Alternatively, the development of human-like behaviors can be facilitated by raising individuals of evolutionarily distant species in the human social environment. Such an example comes from the “Alex project” in which an African gray parrot provided evidence for conceptual quantitative ability (Pepperberg, 1987), social learning, and communicative abilities (Pepperberg and McLaughlin, 1996), in addition to remarkable linguistic skills (Pepperberg, 1991, 1992). These studies clearly argue that tamed animals are being shaped (in the psychological sense of the word) by their human environment. Human handling ensures very complex stimulation which may lead to the development of such complex behavioral and/or cognitive skills that are unobserved in natural environment (Bering, 2004). However, since the captive environment is ecologically irrelevant for the subject’s individual development, it is unclear how the process of socialization (enculturation) affects cognitive development and the emergence of different cognitive skills in these cases (Gomez, 2004).

Although many different species have been used for human–animal comparisons to model one or another aspect of the “hominization” process, there seems to be no perfect solution. For analyzing a wide spectrum of

interacting phenotypic features a “multifunctional” species would be needed that shares an evolutionary and developmental history with humans by living in a similar environment.

C. THE DOG AS A CANDIDATE FOR COMPARATIVE STUDIES

On the basis of recent experimental evidence (for reviews, see [Miklósi, 2007](#); [Miklósi et al., 2004](#)) it has been argued that the dog presents a useful subject for the comparative study of human social evolution ([Hermann et al., 2007](#)) and this species may be the “new chimpanzee” for studies of comparative social cognition ([Bloom, 2004](#)). There are several reasons for why dogs and not other species, including other domestic animals could be a primary target for convergent modeling ([Table II](#)).

1. *The Dog Is Unique Among Domesticated Species*

Although a handful of animal species have come into contact with humans through the process of domestication, the dog is unique. The dog’s origin dates back earlier than that of any other domestic species ([Savolainen et al., 2002](#)) and dogs have survived in various niches provided by humans. Many argue that in the last 15,000–20,000 years dogs invaded the human niche by displaying traits which enhanced their survival in human groups (e.g., [Paxton, 2000](#); [Schleidt and Shalter, 2003](#)). Unlike other domestic species, dogs are used and probably have been selected for many different functions in human groups including such “ancient” roles as hunting or guarding ([Clutton-Brock, 1995](#)).

TABLE II
A POSSIBLE UTILIZATION OF DOGS IN COMPARATIVE INVESTIGATIONS (BASED ON [MIKLÓSI, 2007](#);
[TIMBERLAKE, 1993](#))

		Genetic relatedness	
		Low	High
Ecological relevance	High	Dog versus human (e.g., communicative behavior) <i>Convergence</i>	Among subspecies of wolf or wolf versus coyote and jackal <i>Microevolution</i>
	Low	Dog versus human (e.g., manipulating ability) <i>Classification</i>	Wolf versus dog (e.g., territorial behavior) <i>Homology</i>

The table shows that the nature of comparisons depends on the behavioral trait in question but will in many cases provide complementary information.

and more “novel” ones like assisting disabled people (James and MacDonald, 2000). They provide also emotional support (Wells, 2004) and participate in therapeutic programmes (Odendaal, 2000).

Although little is known about how early stimulation affects the development of dog–human relationship, dogs seem to be predisposed to develop close contact with humans (Gácsi et al., 2005) and human social environment seems to provide a natural niche for dogs (Miklósi, 2007). This is true, despite the fact, that the levels of socialization among dog and human populations are highly variable, ranging from stray dogs that fend for themselves in or around villages and live in very loose contact with humans to others that spend their life as pets in homes with their human owners. Even if some dog populations have lost most of their direct contact with humans, living as feral animals for many generations, the interspecific contact can be reestablished rapidly because the genetic variability between pet dogs and stray or feral dogs is smaller than the environmental variability causing behavioral differences in these phenotypes (Boitani et al., 1995). Since pet dogs can revert to feral life within a few generations (Daniels and Bekoff, 1989), the reverse is possibly also true for feral animals. The lack of an appropriate social environment can also cause irreversible effects on social behavior toward humans in the case of both dogs (Scott and Fuller, 1965) and humans (Candland, 1993).

Evolutionary parallels can be observed in cats or horses, where the domestication process has contributed to their adaptation to the human environment. However, in these noncanine cases, the transition from the wild to the domesticated is likely to represent an earlier state of domestication than is the case for dogs (Bradshaw and Cook, 1996; Bradshaw et al., 1999).

2. *Comparison with the Ancestor Is Important for Convergent Modeling and the Dog Has a Living Ancestor, the Wolf (Canis lupus)*

Dogs offer a unique opportunity for making behavioral comparisons not only with the “niche mate,” the human, but also with the living ancestor, the wolf. The wolf provides a very useful comparative background, because we assume that the convergent skills of extant dogs are derived from homologous traits of the wolf (Kubinyi et al., 2007). For example, wolves show complex social behavior involving cooperation in hunting and parental care, expressive means of communication, and context-dependent dominance relationships (Mech and Boitani, 2003). Presumably, the presence of these skills facilitated the successful adaptation of the dogs’ ancestor to the human social environment and served as the basis for the emergence of specific social behaviors. In our view, the divergence of dogs and wolves involved a process in which the emergence of the dog was accompanied by

increased sociality, cooperativeness, and communicability in the anthropogenic environment analogous to the changes that took place during hominization (i.e., the divergence of the *Pan-Homo* clade).

3. *The Dog Represents a Natural Experimental Model and They Are Less Exposed to Risk of Welfare and Sample Size Problems*

Apart from the evolutionary and developmental arguments elaborated above, this model has many practical advantages. Dogs sharing our life as companions are not only exposed to an environment that shares many physical and social factors that influence human life but observing free-ranging dogs in their natural environment allows for setting up situations in which the subjects can be tested in a rigorous manner. This includes the possibility of comparing directly the behavior of dogs and humans using similar experimental protocols without removing the subjects from their natural environment (e.g., [Lakatos et al., 2009](#)). This method has the potential to achieve higher external validity owing to a theoretically unlimited number of subjects.

In addition, the life history of dogs reveals important parallels with humans, which makes the dogs a valuable subject also for applied disciplines of biology. For example, recent studies have advocated the use of dogs as natural models of human psychiatric conditions ([Overall, 2000](#)) or aging ([Milgram et al., 2002](#)). These approaches rely heavily on the evolutionary convergence of the two species in combination with proximate causal factors such as unnatural (or lack of) social experiences causing malformation of social behavior or the extension of life expectancy in some dog populations due to increased protection from environmental challenges.

IV. STUDYING DOG–HUMAN PARALLELS

Human–dog comparisons have already been initiated long ago (e.g., [Scott, 1992](#); [Scott and Fuller, 1965](#)), especially with regard to social behavior. However, these authors did not make explicit whether the comparisons were built upon a presumed homologous or convergent relationship. Based on evidence pointing to temporal and geographical coincidence between the emergence of mankind and dogkind, others have also noted that the evolution of the dog–human relationship was “closely woven” ([Paxton, 2000](#); [Schleidt and Shalter, 2003](#)), and analogies have been argued for in the case of social-communicative skills ([Hare and Tomasello, 2005](#)) and personality models ([Jones and Gosling, 2005](#)).

A. A NEW APPROACH

Either explicitly or implicitly, recent enthusiasm for studying dogs reinforces the view that this animal species can provide a unique possibility for modeling human behavior. The significance of identifying evolutionary convergence between dogs and humans is that this makes it possible to draw inferences from dog evolution to human evolution regarding the factors that contributed to the rise of human-specific behaviors. However, whilst the aforementioned dog–human comparisons focus on single behavioral traits, here we propose a system theoretical approach. This aims at finding out whether and how the interaction between separate behavioral changes leads to the accumulation of social skills that could resemble in many respects the human social behavioral system. We suggest that the comparative study of social cognition in dogs has the potential to answer questions regarding the functionality of human behavioral components and the following hypothesis could provide an operational framework for this.

1. *The Working Hypothesis*

The three main dimensions of the Human Behavior Complex (sociality, behavioral synchronization, and constructive skills) are assumed to have undergone changes after the *Pan-Homo* split. Taking a behavioral evolutionary perspective, the divergence of the dog from the wolf represents steps taken in the same direction of increased sociality, cooperability, and communicability as has been observed in the case of the *Pan-Homo* clade. As a result of this evolutionary parallel, dogs possess a set of functionally analogous skills corresponding to that of humans, which can be derived from homologous traits of the wolf. Although the time scale is evidently different (i.e., wolf–dog separation took place a few tens of thousands of years ago, whilst the *Homo*-line diverged 6 million years ago), in our view the evolution of dogs mirrors some aspects of hominization. It follows from this that many social skills in dogs have undergone convergent evolutionary changes (Miklósi et al., 2004) and the study of the behavioral convergences between dogs and humans offers a comprehensive framework for understanding the evolutionary emergence of human social behavior (Fig. 1). Naturally, we are aware that dogs cannot fully mirror the Human Behavior Complex because of a number of evolutionary constraints including differences in anatomy and cognitive processing. Convergent behavior modeling emphasizes the surface similarity of the behavior, and investigates the extent of the functional resemblance between humans and dogs, without making specific assumptions regarding the underlying cognitive capacities and physiological mechanisms controlling these skills.

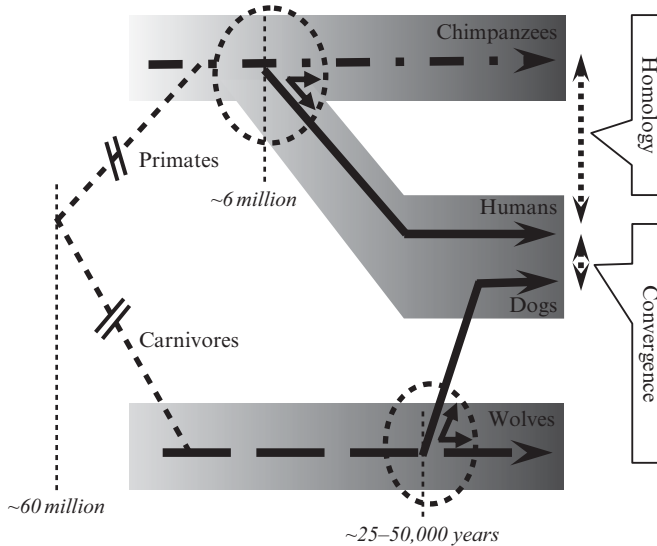


FIG. 1. Divergent and convergent evolution in the Canidae and Hominidae. Although at different time scales it is assumed that behavioral evolution in both cases was subjected to similar selective pressures which resulted in the emergence of convergent social features shared by humans and dogs, which distinguish them from chimpanzees and wolves, respectively. Accordingly, the wolf-dog split can be regarded as a model for early behavioral divergence in the *Pan-Homo* clade (based on Miklósi, 2007).

V. HOW TO IDENTIFY AND UTILIZE CONVERGENT BEHAVIORS BETWEEN DOGS AND HUMANS?

On the basis of the above working hypothesis, we offer a step-by-step procedure by using examples from different aspects of social behavior because, at present, no single trait has yet been subjected to sufficiently detailed analysis.

A. DECOMPOSITION OF DOG BEHAVIOR INTO DISCRETE, FUNCTIONALLY SEPARATED COMPONENTS

To identify convergent behaviors between dogs and human first we need to decompose the behavior of dogs into separate traits patterned after the Human Behavior Complex, and evaluate these behavioral components in comparison to humans. Functional correspondence of dog and human social behaviors cannot only be expected based on their shared evolution and development, but has already been confirmed by empirical evidence in cases of some behavioral traits.

For example, the Human Behavior Complex indicates that increased sociality has led to behavioral scenarios in which intensive gestural communication both facilitates joint collaborative group actions and ensures effective knowledge transfer in the form of teaching. Humans, even in early infancy, show special sensitivity to such “ostensive” cues that signal the teacher’s communicative intention and are able to fast learn the contents of communicative interactions through a human-specific social learning system called natural pedagogy (Csibra and Gergely, 2006). Such a disposition prepares infants to efficiently learn from adults in wide range of situations (Gergely et al., 2007; Topál et al., 2008). There is accumulating evidence that dogs are also able to display some of the abilities required by the receptive side of teaching interactions: sensitivity to the human’s communicative intent (e.g., Kaminski, 2009; Pongrácz et al., 2004) and to the referential character of human cuing (e.g., Riedel et al., 2008; Soproni et al., 2001). In line with these observations, those skills that makes the dog able to show relevant responsiveness to human communicative gestures, could be regarded as a functionally separated component of the dog behavior repertoire that is comparable to that of human’s skills. Future research could find out what are the shared and distinctive traits in comparison with wolves and human infants?

B. INTRASPECIFIC COMPARISON OF FUNCTIONALLY CORRESPONDING BEHAVIOR BETWEEN DOGS LIVING IN A HUMAN ENVIRONMENT AND WOLVES LIVING IN THEIR NATURAL HABITAT (OR UNDER SEMINATURAL CONDITIONS)

The ethological approach holds that species comparisons should be based on natural behavior, which is by definition displayed under natural conditions. Behavioral differences that could be the result of evolutionary/functional and/or developmental origin could provide the starting point for further investigations. Notwithstanding the fact that such research projects have a considerable history in ethology (Fentress, 1967; Fox, 1971; Frank and Frank, 1982), systematic comparisons are lacking because in the case of both wolves and dogs, the ideal circumstances for data collection are difficult to establish. The shyness of wolves and their long traveling distances prohibit close observation in nature and captive observation often produces behavioral artifacts. Similarly, with a few exceptions intraspecific observations on dogs are simply lacking. Nevertheless, the few relevant studies that exist provide a good starting point in the case of play (Bekoff, 1974), vocalization (Feddersen-Petersen, 2000), or agonistic behavior (Goodwin et al., 1997). Comparing the human-related social behavior of dogs to intraspecific wolf behavior would be necessary to investigate

whether dog–human similarities reflect indeed convergences or rather homologous traits shared by wolves, dogs, and humans (and probably other social mammals).

C. INTERSPECIFIC BEHAVIORAL COMPARISONS OF HAND-REARED WOLVES AND DOGS

Raising wolves and dogs identically in human environment, and comparing their human-related behavior is crucial to account for possible environmental effects. It has been often argued (e.g., [Udell et al., 2008](#)) that the behavior of dogs is mainly the result of environmental influences dominated by human intervention. If the environment of wolves and dogs is equalized then the remaining behavioral differences could be explained in terms of inherited factors (and/or maternal prenatal influences). Although there have been a number of attempts for interspecific comparisons (e.g., [Frank and Frank, 1982](#); [Hare et al., 2002](#); [Udell et al., 2008](#)), there has been huge variability in the socialization of both the wolves and the dogs. This could have confounded the observed differences.

In a recent series of studies using extensively socialized hand-reared wolves and dogs, behaviors were compared in a divergent array of contexts involving humans and dogs, including social preferences ([Gácsi et al., 2005](#)), attachment to humans ([Topál et al., 2005a](#)), interspecific gestural communication ([Udell et al., 2008](#); [Virányi et al., 2008](#)), and interaction with humans in problem solving situations ([Miklósi et al., 2003](#)). These studies point to important species-specific differences that can be attributed, at least in part, to the dogs' evolutionary adaptation to the human niche.

D. COMPARING DOGS AND HUMANS IN FUNCTIONALLY SIMILAR SITUATIONS

Based on behavioral differences between dogs and wolves found in steps 2–3, one could predict functional similarities between humans and dogs. In search for evolutionary convergent behaviors in dogs and humans the direct comparison of the two species is indispensable. There are various possibilities for comparing human and dog behavior because of the close similarity in the developmental environments and the relative absence of experimental or technical limitations for both observational and experimental work (in comparison with apes). One can also control for assumed cognitive skills and/or durations of social experience and utilize human children for comparison, or one can compare directly the behavior and performance of adults in both species.

For example, the dogs' ability to rely on various forms of human directional gestures can be directly compared with corresponding skills of human infants at various ages. The results show that dogs' performance can be equated with that of 1.5–2-year-old children (Lakatos et al., 2009). Also, like 3-year-old children, dogs can discriminate between behaviorally very similar visual cues when they differ in referential function only and not in their effectiveness as discriminative cues (Povinelli et al., 1999; Soproni et al., 2001). Moreover, pet dogs and 2.5-year-old children show functionally similar behaviors in tailoring their communication to others' state of knowledge in an "out-of-reach reward" task (Virányi et al., 2006).

E. COMPARISON OF UNDERLYING CONTROLLING FACTORS AT THE BEHAVIORAL, PHYSIOLOGICAL, AND GENETIC LEVELS

Once a reasonable level of functional convergence has been established, one might search for underlying causal factors (Miklósi et al., 2007). Dogs provide a very interesting model for such an approach because they come in genetically partially isolated populations and also because, within limits, there is the possibility of manipulating their physical and social environment. This provides a natural scenario for testing interactions between both genes and genetic background or genes and environment. Such investigations could reveal that the controlling factors behind convergent traits can be different even while sharing some basic features. Such a case has been revealed recently where activity/impulsivity in dogs (measured by an application of a human ADHD questionnaire, Vas et al., 2007) seems to be influenced by similar genetic factors (a gene coding for dopamine receptor, DRD4) while very probably the precise underlying genetic mechanism is different (Héjjas et al., 2007a,b, 2009). These results and the recent publication of the dog genome (Lindblad-Toh et al., 2005; Parker et al., 2004) offer new opportunities for the utilization of dogs in the understanding of causal factors in human diseases and phenotypic malformations (Sutter et al., 2007).

VI. USING THE APPROACH: ATTACHMENT AS A CASE FOR CONVERGENT BEHAVIOR

Wickler (1976) defined attachment as a long-lasting attraction to a particular set of stimuli, which manifests itself as particular behaviors directed toward or performed in the presence of these stimuli ("objects of attachments") in addition to maintaining proximity to the relevant stimuli over a period of time. This operational description is consistent with Bowlby's (1972) assumptions that attachment is a behavior-controlling structure,

which evokes a particular set of actions in stress situations (e.g., separation from the object of attachment). In practice, the existence of attachment-systems is usually decided upon fulfillment of certain behavioral criteria (Rajecki et al., 1978). In general, the organism should display separation stress in the absence of, seek proximity and contact with, and show specific greeting behavior in the presence of the object of attachment, which is at least quantitatively different from similar actions performed toward a stranger. In the following, we argue for behavior convergence in dogs and humans in the case of attachment. However, the lack of extensive research in this area means that many questions still remain to be answered.

Step 1: Is attachment a separable component of dog behavior?

It has often been assumed that humans live in a natural relationship with dogs which can be interpreted in the framework of social attachment (e.g., Serpell, 1996). A range of questionnaire studies has established that owners regard pet dogs as family members (e.g., Albert and Bulcroft, 1987). Owners attribute cognitive and emotional skills to their dogs that are in many respects similar to a 6-year-old child (Rasmussen and Rajecki, 1995) and owners are inclined to describe the relationship with their dog in terms of attachment (Poresky et al., 1987). This anthropomorphic attitude gains some support from observational studies revealing analogies in child–human and dog–human interaction (Prato-Previde et al., 2006) including verbal communication, such as the use of “motherese” and “doggerel,” respectively (see Hirsch-Pasek and Treiman, 1981; Mitchell, 2001). Finally, at the behavioral level, Topál et al. (1998) were the first to reveal child–dog analogies in the pattern of attachment, which have since been replicated in other laboratories (e.g., Marston et al., 2005; Prato-Previde et al., 2003). Results show a characteristic selective responsiveness to the human caregiver (owner) in both dog puppies and adult ones, and this supports the view that attachment is a functionally distinct component of the social behavior of the dog.

Step 2: Is there evidence for intraspecific attachment behavior in dogs or wolves?

Very few studies reflect on the attachment-like relationships among wolves in their natural habitat or among feral dogs. For example, LeBoeuf (1967) describes a group of dogs reared together and associations between pairs of dogs but this was related to the sexual context, and the presence of attachment relationship was not implicated. It seems that, except for the relatively early phase of individual development, neither dog puppies nor wolf cubs show specific attachment to their mother. Mech (1970) reported that proximity and contact seeking behavior toward the mother gradually decreases after weaning in gray wolf cubs at 6–8 weeks of age, and attachment is observed mainly toward the pack as a whole

rather than a specific individual (Rabb et al., 1967). Experimental studies revealed that in 2-month-old dog puppies the bitch plays only a minor role in reducing the effect of separation stress (Elliot and Scott, 1961; Ross et al., 1960) and in choice situations puppies do not show preference for the mother in comparison with an unfamiliar bitch (Pettijohn et al., 1977). In sum, although well-designed comparative studies are lacking, both dogs and wolves seem to fulfill the operational criteria for intraspecific attachment toward their mother only in early puppyhood.

Step 3: Are there interspecific behavioral differences in attachment behavior of hand-reared wolves and dogs toward humans?

Wolf puppies that are socialized by humans show species-specific affective behaviors toward their caregivers. However, unlike dogs, gray wolves exposed both to conspecifics and humans showed a preference for the canid partner if they were offered a choice (Frank and Frank, 1982; Gácsi et al., 2005). In a recent study (Topál et al., 2005a) we have argued that if the emergence of attachment is based exclusively on social experience during early exposure to humans then wolves reared in extensive human social contact should show attachment behavior toward their human caregivers that is similar to that observed for dogs. Results show, however, that in contrast to 4-month-old dog pups, gray wolf cubs of the same age did not fulfill the criteria for attachment (Topál et al., 2005a). Despite being hand-raised and socialized to an extreme level (in contact with their owners 20–24 h/day for the first 3–4 months of their life), these hand-reared gray wolf pups did not seem to discriminate between their caregiver and a stranger greeting them when left alone in an unfamiliar enclosure. It seems that unlike dogs, the human caregiver does not act as a “secure base” for wolves in stressful situations.

These observed differences between wolves and dogs provide little support for dogs' attachment to humans being either exclusively the outcome of extensive human socialization or resulting from species-specific differences in the rate at which the development of attachment system operates (heterochrony, see Coppinger and Coppinger, 2001; Goodwin et al., 1997). This is so because even very young wolves do not show attachment behavior toward their human caregivers. Moreover, this is in contrast to widely held views since both processes have hitherto been implicated heavily in explaining the development of dog–human attachment. Such theories have assumed that the behavior of dogs shown toward the owner is derived directly from the puppy–mother relationship in wolves, supposing a behavioral homology between dog and wolf behavior.

It is not yet clear whether the development of attachment toward humans is the result of a general mechanism with low specificity for accepting social stimuli/objects as group mates, or whether the continuous selection in the

human environment might have resulted in more specific changes. Regarding the genetic aspects of attachment, recent research based on comparisons of closely related species (prairie vole vs mountain vole) has suggested that small and well-defined changes at the neurogenetic level (i.e., alteration in the oxytocin and vasopressin receptor genes) can lead to marked alteration in social affiliative behavior (for a review, see [Insel and Young, 2000](#)). One may assume that similar changes should be occurring in dogs leading to the “evolutionary” emergence of attachment to humans. In the lack of experimental evidence, however, we can only speculate about this hypothesis.

Step 4: To what extent do dogs and humans show functionally similar patterns of attachment behavior?

An experimental method for studying behavioral criteria of human infant–parent attachment has been developed by [Ainsworth \(1969\)](#) (Strange Situation Test). She found that separation from the caregiver in an unfamiliar environment evokes anxiety in infants which is behaviorally manifested in proximity seeking. Moreover, the activated attachment system upon reunion with the mother manifests in different forms of contact seeking behaviors. This method has also been utilized to test attachment behavior in dogs ([Topál et al., 1998](#)) offering direct comparisons between the behavioral manifestation of attachment behavior in dogs and human children.

Results have confirmed functional behavioral similarities between dogs and children. Dogs displayed a specific reaction toward their owners, but not toward a stranger, by looking for them in their absence and making rapid and enduring contact upon their return. They also preferred to play with the owner, and decreased play activity in the absence of the owner ([Prato-Previde et al., 2003](#); [Topál et al., 1998](#)). Follow-up work provided evidence that this pattern of attachment is stable over at least 1 year and is independent of the peculiarities of the testing location ([Gácsi, 2003](#)).

An important further analogy to the human case has been revealed by observing the emergence of attachment behavior in shelter dogs. These observations suggest that dogs that have been deprived of human contact (adult shelter dogs) are able and motivated to initiate a new relationship rapidly after a short duration of social contact with humans ([Gácsi et al., 2001](#)). In a similar experiment, [Marston et al. \(2005\)](#) found that physical contact (massage) was more effective than obedience training as a form of handling in evoking patterns of attachment toward humans.

Other observations suggest that similar to the case of human infants ([Matas et al., 1978](#)), dog–human attachment provides a kind of scaffolding for the emergence of various social behaviors in cooperative and

communicative interactions (Topál et al., 1997). In contrast to the autonomous problem-solving behavior of the wolf (Frank, 1980), dogs show a predisposition toward engaging in joint activities with human members of their group (see also Miklósi et al., 2003).

In summary, compared to human children, pet dogs show functionally similar attachment behaviors toward their caregiver. Moreover, unlike other nonhuman species, dogs retain “infant-like” attachment behavior and are able to reestablish novel attachment relationships in their adulthood.

Step 5: Is there evidence for similarity in the underlying genetic and/or physiological controlling factors of dog and human attachment behavior?

Attachment behavior is usually evoked by situational stress which has evident physiological correlates. In human infants, separation from the attachment figure results in elevated levels of cortisol and heart rate (Spangler and Grossmann, 1993). Similarly, separation from the owner induces emotional stress in dogs (Maros et al., 2008; Palestrini et al., 2005), which is indicated by increased heart rate frequency. Interestingly, these changes can be reversed by specific effects. For example, Tuber et al. (1996) found that in novel environments the increased level of cortisol can be reduced by the presence of a familiar human but not by a familiar dog. In a similar vein, petting by a familiar human has a relaxing effect (release of beta-endorphin, oxytocin, and prolactin, reduction of heart rate) on both parties (Odendaal and Meintjes, 2003) and gazing at the owner and other social interaction initialized by the dog can increase the owner's urinary oxytocin concentration as a manifestation of attachment behavior (Nagasawa et al., 2009).

Moreover, one might suppose that convergence in attachment behavior could explain similarities in behavior problems that were described both for infants and dogs (Fox, 1975; Overall, 2000), although the only study conducted so far did not find a direct link between attachment to owners and separation anxiety (Parthasarathy and Crowell-Davis, 2006).

Human attachment studies have shown that different allelic variations of human dopamine D4 receptor (DRD4) gene are associated with different patterns of attachment in infants (Lakatos et al., 2000). Recent molecular genetic investigations have revealed the presence of an analogue polymorphism in the dog DRD4 receptor gene (Inoue-Murayama et al., 2002), which implies the potential for similar gene-behavior associations in this species (Héjjas et al., 2007a,b).

Taken together, our scattered evidence suggests that changes in genetic and physiological mechanisms might have accompanied the emergence of human-like attachment behavior in dogs.

VII. BEHAVIORAL PARALLELS BETWEEN DOGS AND HUMANS: THE DOG BEHAVIOR COMPLEX

On the basis of evidence suggesting that dogs' behavior became to some extent functionally similar to the most important aspects of the human behavior, we propose that the model developed for the description of human behavior traits (Human Behavior Complex, see above) might provide a useful framework with which to conceptualize evolutionary changes in dogs. The Dog Behavior Complex defines those components of dog behavior for which there is evidence that they have contributed to the species' success in the human social niche. Obviously, dogs cannot fully mirror the Human Behavior Complex because of evolutionary constraints (e.g., lack of linguistic skills in dogs). In spite of this, behavioral research so far has provided ample evidence that there is a parallel between the human and Dog Behavior Complex. In the following, we provide a short summary of the available evidence concerning human-oriented social behavior in dogs, presented within the framework of the human behavioral complex.

A. SOCIALITY

Anyone who has raised wolves and developed a close relationship with them has noticed major differences between human-oriented social behavior in dogs and wolves (e.g., [Fox, 1971](#); [Frank and Frank, 1982](#)). These differences include both affiliative and agonistic aspects of social behavior that emerge during the early stages of development and become more pronounced during adult life. So far, three main factors have been studied which influence dog-human social relationships: attachment (see above, [Section VI](#)), social attraction, and agonistic behavior.

1. Social Attraction

The behavioral manifestation of group cohesiveness and intragroup attraction that holds groups together can be defined as social attraction ([Oakes et al., 1998](#)). In contrast to attachment, which can be regarded as individual personal attraction, social attraction is based on "liking of each other as group members," not as unique individuals. For both human and nonhuman species, attraction to conspecifics is a prerequisite for forming complex social groups.

While there is an array of possible mechanisms to achieve mutual attraction among conspecifics, the situation is more complex if such attraction is expressed toward heterospecifics. The idea that dogs might have some predisposition to be attracted to humans has been around for a long time. Earlier it had been observed that dog puppies develop preferences toward

humans after only a brief exposure (Stanley and Elliot, 1962) and despite being punished for social contact (Fisher, 1955). Comparative experiments provided various types of evidence that overall dogs show a stronger attraction toward humans than wolves show toward humans (Frank and Frank, 1982; Zimen, 1987).

2. *Agonistic Behavior*

Wolves are often portrayed as being fiercely aggressive animals, in contrast to the gentle manner of “man’s best friend.” Both classic studies (Scott and Fuller, 1965) and recent accounts (Hare et al., 2005) have assumed that selection has led to reduced aggressive behavior in dogs (see also Price, 1999). In contrast, other observations on dog and gray wolf puppies does not provide support for a generally lower level of aggression in the former, as dog puppies have been found to display agonistic behavior more frequently than wolves of similar age (Feddersen-Petersen, 1986). However, even wolves with extensive socialization history were more likely to growl at or bite the caretaker who handled them during the experiment (Gácsi et al., 2005). This could have been a manifestation of increased defensive aggression in wolves indicating a lower threshold for socially inflicted constraints.

With regard to the sociality component of the Dog Behavior Complex, then, we argue that both the generally lower level and increased controllability of aggression, and the more intensive social relationships, contribute to the development of closer interspecific ties between humans and dogs.

B. SYNCHRONIZATION

Synchronization can be defined as processes leading to behavioral or motivational/emotional conformity. Achieving behaviors related in time (synchrony) is essential for group cohesion (Engel and Lamprecht, 1997). Thus, the ability for behavioral synchronization probably enhanced the ability of dogs to maintain close relationships with humans. Scant research on these issues has revealed so far four aspects of dog behavior: emotional synchronization, social learning, rule following, and complementary cooperation.

1. *Emotional Synchronization*

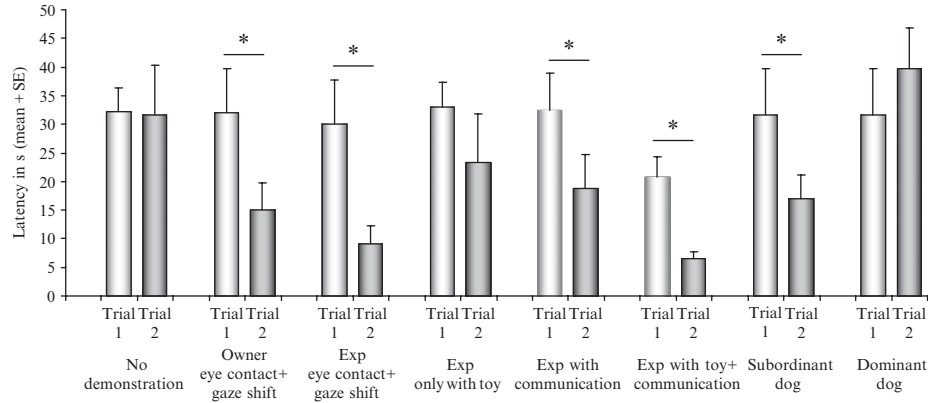
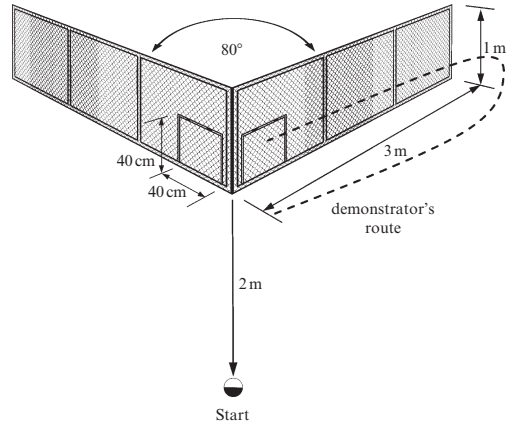
Although evidence is very limited, it is likely that dogs have the ability to show emotional synchronization by attending to various visual or acoustic social signals emitted by humans. For example, a recent study provided some evidence of synchronization during heterospecific play when various play signals seemed to have the potential to evoke play behavior from the

other, probably through change in mood (Rooney et al., 2001). Similarly, when approached by an unfamiliar person showing definite signs of friendliness and threat in succession, dogs show rapid changes of emotional and behavioral response in accordance with the human's attitude (Vas et al., 2005). Such emotional synchronization is a bidirectional process. There is a growing literature indicating that the mere presence of dogs or interaction with them has an effect on the emotional state of humans (see Hart, 1995 for a review; Friedmann, 1995; Wilson, 1991). As bodily contact in the form of "social grooming" is a dominant behavior for expression empathy in humans, dogs could have been selected for similar tendencies (e.g., the mutual relaxing effect of petting in Odendaal and Meintjes, 2003).

2. Behavioral Conformities Achieved by Social Learning

a. Learning from conspecifics Social learning is potentially an efficient method of obtaining information by observing conspecifics. In the dog there is some evidence that observing conspecifics can lead to improved performance (Kubinyi et al., 2009). Slabbert and Rasa (1997), for instance, demonstrated that young police dog puppies left with their mother until 3 months old and provided with the opportunity to observe the bitch searching for narcotics, displayed superior performance when learning the same task later by comparison with control pups. In addition, puppies can learn from each other: observing a littermate pulling a small cart on a string facilitates the emergence of the same behavior later (Adler and Adler, 1977). In a more recent study dogs even seem to evaluate the action of a conspecific demonstrator (Range et al., 2007) and, similarly to human infants (Gergely et al., 2002), imitate the demonstrator's action selectively on the basis of whether or not the observed behavior was "rational."

b. Learning from humans Dogs can use, however, also human behavior as a cue for selecting functionally similar behavior (Kubinyi et al., 2003a; Miller et al., 2009; Topál et al., 2006a) and for obtaining information to solve certain problems. Findings suggest that pet dogs are not particularly good at going around a V-shaped fence (Fig. 2) in order to get to a target (food or toy). In contrast, much improvement in performance was found when dogs were allowed to watch a human demonstrator making the detour (Pongrácz et al., 2001b). Further, dogs were able to rely on this information when they had opposing experience. In one experiment, dogs were allowed to get the food/toy through an opening in the fence at the tip of the "V." If they were prevented from choosing this route by closing the opening, the performance of most dogs fell below that showed by naïve individuals.



However, observer dogs could overcome this bias and develop the habit of detouring rapidly, which shows that they were able to use the information provided by the humans (Pongrácz et al., 2003a).

Dogs seem to learn differently from humans than from conspecifics (Pongrácz et al., 2008). They easily learn the detouring from another dog but a human walking around the fence can enhance their later performance only if she/he is talking to the dogs during demonstration (Pongrácz et al., 2004). The influence of human communication on the dogs' decisions is even more conspicuous when it is possible for the individual to choose between two exclusive behavioral actions, for example, if there is a conflicting situation to behave either according to earlier human actions or provide a "rational" solution to a problem. In a recent experiment dogs were observed in a two-way choice task, in which human provided information about the location of the reward in different ways (showing the content of either the empty or the baited container) and using different cues of communication (Erdőhegyi et al., 2007). We found that for the dog, the function of human demonstration is probably not transferring knowledge *per se* but transferring those behavior actions that can lead to effective behavioral synchronization (Erdőhegyi et al., 2007).

3. Rule Following

De Waal (1996) and others assume that obedient behavior of dogs and their "desire to please us" is partially based on their social skill at comprehending and following social rules (Bekoff and Allen, 1998). There is some evidence that dogs are inclined to follow social rules of the group in both the short and long term. One simple form of rule following is when the

FIG. 2. Dogs are not especially good at making detours. In a series of experiment Pongrácz et al. (2001b, 2004, 2008) studied how quickly the dog learns that it has first to move off from the target in order to reach it at the end of the route. Naïve dogs could develop the habit of detouring by trial-and-error learning only after 4–6 trials. In contrast, dogs improved their performance after watching a detouring human demonstrator. Importantly, human demonstrations were more effective when the detour demonstrations included cues of communication (addressing the dog, eye contact with the dog, gaze shifts between the dog and the target object). Dogs could also utilize detour demonstrations of another dog (group mate) depending on the subject's relative dominance rank with the demonstrator. Subordinate dogs displayed significantly better performance after having observed a dog demonstrator in comparison to dominant dogs. Pairs of columns indicate the latency of making the detour (mean + S.E.) in the first trial (trial 1—naïve subjects) and in the second trial (trial 2—after having observed a demonstration) of different experimental conditions. Drawing of the fence used for the social learning test is also shown. Detours were demonstrated either by the owner, or by an unfamiliar experimenter or by a familiar dog. Significant differences compared to the first trial are indicated with * $p < 0.05$.

individual develops and maintains habitual behavior in a social context in relation to its partner. The function of this form of social influence might be to avoid conflicts in the group and to cooperate in common actions without any deeper insight into the knowledge content of another's mind.

We have also found some indication for this in experimental situations developed for the study of social learning. After observing the demonstration of detouring and having detoured the V-shaped fence with a closed opening several times, dogs showed only a gradual inclination to take the shorter route to the target if the opening became available. Further analysis suggested that dogs noticed the change because they looked more frequently at the opening than they had done earlier (Pongrácz et al., 2003b). Nevertheless, the dogs followed their social tendency and only gradually gave up on this habit and shifted to the use of a more effective behavior to obtain the hidden food by walking through the opening.

In another experiment we tested whether dogs would adopt spontaneously a novel, arbitrary (actually pointless) behavior as a result of interaction with their owner. We asked dog owners to change their route after arriving back from walking the dog (Kubinyi et al., 2003b). Instead of taking the shortest route to their flat, they had to take the dog off leash and make a short detour leading away from the entrance door. They were instructed to ignore the dog during this detour until they arrived back at the door. Over a period of 3–6 months this action was repeated 180 times and the dogs gradually developed a behavior corresponding to their owners' demonstrations: half of the subjects not only escorted the owner but also overtook them and finished the detour earlier than the owner. These results indicate that after a certain amount of repetition, dogs can form expectations about the behavior of the human. This ability to anticipate the action of the other, contributes also to the manifestation of synchronized behavioral interactions between man and dog. At a behavioral level, social anticipation can also be interpreted as a mechanism for reducing conflict in the course of interaction between two parties.

Similarly, we have also explained dogs' behavior in terms of rule following when in an object permanence task (Fig. 3). We found that dogs are able to track the trajectory of an object even if it was concealed in a container (invisible hiding tasks—Watson et al., 2001). After participating in several invisible hiding trials, the object was hidden in full view of the dogs at a new location. Results showed that many subjects, in this case, showed seemingly erroneous behavior. That is, they were more inclined to seek out the hidden object at various locations rather than to go directly to the location of the object which they knew. Repeating a similar type of experiment with children and adults gave similar results, although the proportion of “searchers” in the “game” hiding trial was somewhat smaller in the case of adults

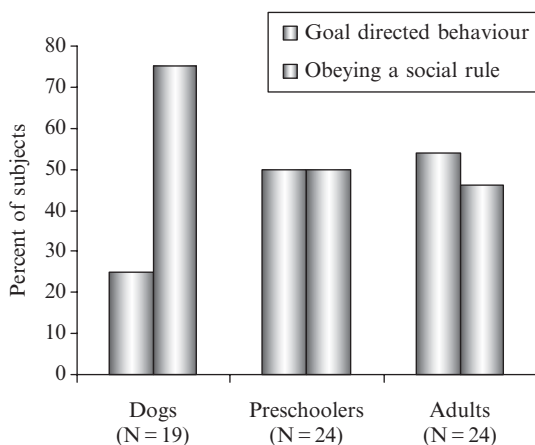
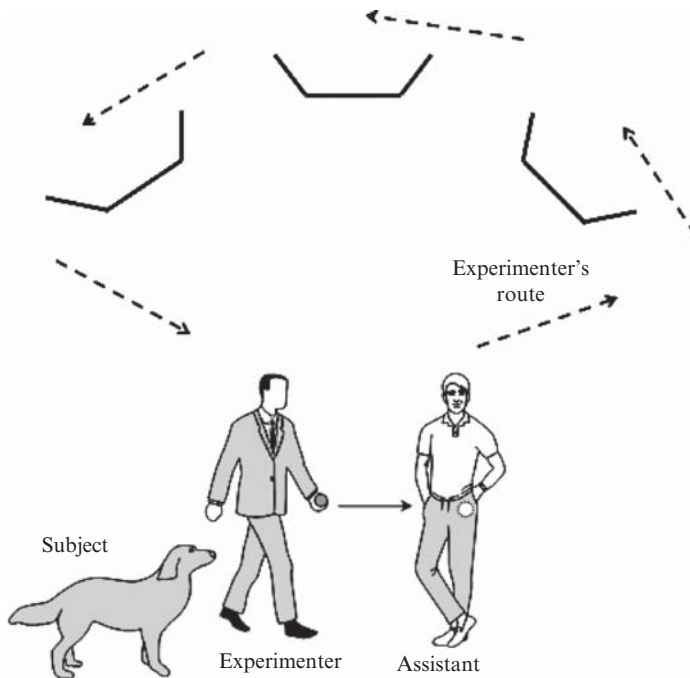


FIG. 3. In object hide-and-search tasks dogs' behavior is controlled by not only their mental representational ability but they can act on the basis of some other search rules. With the participation of a human experimenter the task becomes a sort of social game where the human is doing the hiding and the dog is searching. In a recent study (Topál et al., 2005b), the training phase (hiding the object repeatedly behind one of the identical screens) was followed by a

(Topál et al., 2005b; Fig. 3). On the basis of these observations, we may say that the ability to identify and use social rules that are formed by the interaction with the experimenter during the consecutive object hiding and search tasks may have a significant influence on the performance of both human and dog subjects.

Taken together, it seems that dogs have considerable ability to obtain information of varying complexity by observing their human companion. The accumulation of such social information could play an important role in synchronization of group activities as members of the group can act on the basis of the same knowledge. This could make interactions between companions more easy-going and more efficient.

4. *Complementary Cooperation*

Goals can often be achieved only by cooperative interactions with others in the group. Evidence suggests that interacting dogs and humans establish a complex behavior pattern when performing joint actions (Kerepesi et al., 2005; Rooney et al., 2001). Dogs are not only sensitive to meta-communicative signals (e.g., the play bow) in order to maintain play but also engage in complex “behavioral projects” in order to continue playing (Mitchell and Thompson, 1991). In another study, detailed observations have revealed complex interwoven behavioral interactions between blind persons and their guide dogs (Naderi et al., 2001). Dog-owner dyads surmounted an obstacle course, and determined the ratio of actions initialized by either the dog or the human. Although there was large variation among the dyads on average dogs and human initialized the half of the actions. Moreover, at the individual level we found that the role of the initiator was changed continuously. In most cases neither party initiated more than 2–3 actions in a row, it was most common to relinquish the initialization after one action. Such switching in leadership in addition to the dogs’ ability to perform complementing actions to achieve a joint goal closely resembles cooperative activity described in the case of humans (Reynolds, 1993).

“game” trial: the toy was visibly given to the owner (who hides it in a pocket) and the experimenter took the same route without the target (“shammed hiding”). Results show that majority of dogs performed search behavior in the “game” condition. Such “counterproductive” solution to the task was also observed in humans (both children and adults) and this behavior could be interpreted as the result of accepting social rules (Topál et al., 2005b). Figure shows the schematic representation of the experimental arrangement. Columns indicate the proportion of subjects (dogs, preschooler children, and adults) following goal directed behavior (“getting the object”) or a social rule (“producing search behavior”) when the location of the target object was well known by the subject (“game” condition).

C. CONSTRUCTING COMMUNICATION

When communicating, humans use an infinite number of communicative signals in at least the visual and acoustic modes. In addition, they apply certain signals for initializing and maintaining communication (e.g., eye-contact) and rely on various behavioral cues for recognizing attention. To what extent do dogs demonstrate these features of communication?

1. *Initializing Communication with Humans*

There are some indications that dogs have a strong propensity to initialize communicative interactions with humans, and for this they rely predominantly on visual signals (looking and gaze alternation) which are functionally similar to those used by humans. This pattern of behavior can be revealed in situations where dogs are exposed to insoluble problems in the presence of humans. Under these circumstances, dogs show many forms of behavior (gazing, gaze alternation, vocalization) that direct the attention of the human onto themselves or the problem to be solved (Miklósi et al., 2000). Comparative experiments have shown that this behavior pattern also emerges more readily in dogs than in hand-reared wolves (Miklósi et al., 2003; Virányi et al., 2008). There are also indications that the preference to look at the human develops very early in dogs in comparison to wolves (Gácsi et al., 2005; Fig. 4), which can in principle provide the basis for the emergence of complex communicative interactions between humans and dogs.

2. *Relying on Visual Cues of Human Attention*

The preference to look at the human's face might have led to enhanced skills in reading behavioral cues of human attention in dogs. In a series of experiments we have found that dogs are very sensitive to behavioral cues signaling attentiveness. According to work done by Gácsi et al. (2004) dogs readily discriminate face orientation of the human by approaching him mostly from the direction of the face when retrieving an object (see also Bräuer et al., 2004). Dogs display the same performance when they have the choice to beg from persons turning either toward or away from them, and there is suggestive evidence that they also discriminate open versus closed eyes. Dogs use eye-contact and directed talk provided by humans to infer whether they are addressed in a particular situation (Virányi et al., 2004). In the social learning context, we have found that dogs learn detouring much better if the human uses eye contact and verbal signals to get the attention of the dog (Pongrácz et al., 2004). Findings also suggest that dogs are particularly sensitive to behavioral signals of attention in commanding situations (Call et al., 2003; Virányi et al., 2004).

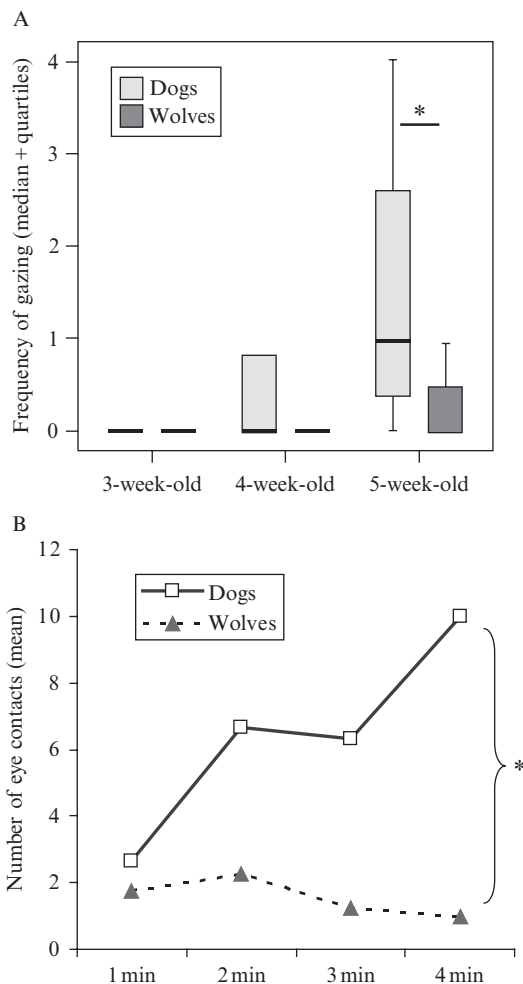


FIG. 4. In the wolf, gazing plays a crucial role in agonistic communication. The use of gazing in intraspecies aggressive interactions in dogs is basically similar to that of described in the wolf (Fox, 1971). However, with respect to nonaggressive communicative interactions dogs differ in their willingness to gaze at the human's face and this difference can be observed in early puppyhood (Gácsi et al., 2005). In contrast to wolf puppies, dogs show a clear preference for establishing eye-contact with humans in a "free approach" test (when puppies were allowed to move freely in the presence of passive "social agents") and in a "reinforced eye-contact" task (when eye-contacts initialized by the puppy was rewarded by the human). (a) the frequency of gazings (number/min) at the human face in 5-week-old hand reared gray wolf and dog puppies in a social preference test (medians + lower and upper interquartile ranges). (b) Mean number of eye contacts of 9-week-old hand reared wolves and dogs with a familiar experimenter during a 4-min-long operant conditioning test. Significant differences are indicated with $* p < 0.05$.

3. *Responsiveness to Human Communicative Gestures*

Recently, intensive research efforts have revealed that dogs can rely on various human bodily gestures as communicative signals. In these experiments dogs have to find hidden food based on cues provided by a human (for a review, see Miklósi and Soproni, 2006). Dogs can use various forms of pointing (e.g., Hare et al., 1998; Soproni et al., 2002), as well as head turning (Soproni et al., 2001) as indications of the location. The performance of dogs in these experiments can be compared to 1.5–2-year-old children (Lakatos et al., 2009), and young dogs are superior to hand-reared wolves (Miklósi et al., 2003), although the latter can also rely on pointing cues after intensive socialization and some training (Virányi et al., 2008; but see also Udell et al., 2008). There is also evidence that dogs can interpret a human pointing gesture even in early puppyhood without any explicit training (Gácsi et al., 2009). Adult dogs are able to rely on pointing types, which lack any discriminative component (Riedel et al., 2008) or require the ability to generalize among contexts (Lakatos et al., 2009; Soproni et al., 2002; Fig. 5). In addition, other experiments have shown that some dogs prefer to rely on the pointing gesture even when they have conflicting visual or olfactory information about the location of the hidden object (Szetei et al., 2003). Recently, it has been shown that dogs are able to rely on a marker used by the experimenter to indicate the correct location of hidden food (Agnetta et al., 2000; Riedel et al., 2006).

4. *“Word Learning” Capacities*

Even if we have only a limited amount of experimental evidence of “word learning” capacities of dogs, in general owners have the impression that their dog comes to understand the meaning of certain verbal utterances, or at least to act as if they possessed this knowledge (Pongrácz et al., 2001a). More recent research seems to provide evidence that both the acoustic composition of the “word” (Fukuzawa et al., 2005a) and the attentional component (Fukuzawa et al., 2005b) associated with the utterance affect the performance of the dog.

Although it is widely known that dogs are able to make associations between verbal cues (words) and an action (retrieval) or an object (Young, 1991; for a review, see also Mills, 2005), there is some suggestion that dogs can make the association between a novel object and its “name” by observing/listening to conversing humans. From language learning experiments, we know that children are very sensitive to such situations. For example, 1.5-year-old children will preferentially associate verbal cues to those objects which were in the visual focus of the adult during emitting the utterance (e.g., Baldwin and Baird, 2001). In a similar experimental situation, known as

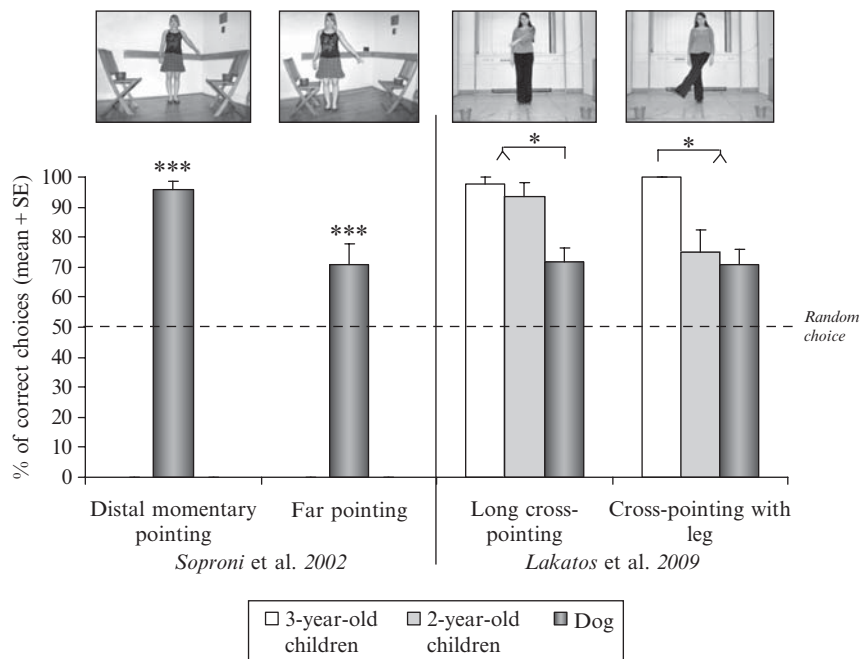


FIG. 5. Comparative investigation of the comprehension of human gestural cues is widely believed to provide useful information on the flexibility of the communicational skills of different animal species (Miklósi and Soproni, 2006). Many assume that distal momentary pointing and other types of directional gestures can be used to measure the subjects' understanding the communicative referential nature of human behavior cues (Hare et al., 2002; Miklósi et al., 1998). Recent evidence suggest that dogs may be able to decode the referential aspect of human directional gestures, and like human children, they show reliably high performance in choice tasks including various types of pointing signals (Lakatos et al., 2009; Soproni et al., 2002). Dogs' and children's performance (percent of correct choices, mean + S.E.) in different types of human pointing tests (based on Lakatos et al., 2009; Soproni et al., 2002). Significant differences compared to random choice are indicated with *** $p < 0.001$, and compared to the performance of other groups are indicated with Φ ($p < 0.05$).

Model-Rival method, Pepperberg (1991) was successful in teaching word-object associations to African gray parrots. Recently, McKinley and Young (2003) presented some evidence that dogs can also learn the name of an object when they have the chance to observe two humans naming the novel object during conversation. Very likely dogs are facilitated in doing this by the behavioral cues of humans indicating attention toward the object, as well as the object being manipulated during the conversation. In an other study, one dog has been shown to base his performance not on human behavioral cues but on previous knowledge about the names of the other familiar objects

(Kaminski et al., 2004). Although there is some disagreement on the interpretation of the underlying cognitive processes (see Bloom, 2004), this dog, knowing the names of about 200 different objects, was able to recognize that a novel utterance indicates the name of the novel object among a set of familiar objects with known names.

5. “Mindreading” Skills

Further interesting observations on dog communication with humans suggest that they might be able to complement information that is missing in the human. Nonverbal variants of experiments used to tap into the ability to recognize knowledge or ignorance in others (Gomez, 2004) have been applied to the dog (Topál et al., 2006b; Virányi et al., 2006). In these tasks, dogs could see a human “Hider” placing a toy object or a piece of food in one of the three identical boxes. Dogs could always know the location of the reward; however, they could get it only by the help of another human, a Helper. Experimental conditions were designed to investigate the “requesting” behavior of the dogs (signaling a baited box which is unreachable to them) on the basis of whether human “Helper” participated in object hiding events or not. Results show that in spite of the dogs’ restricted gesturing abilities subjects modified their behavior adequately to the knowledge of the Helper. Although one could invoke the ability of dogs to take the other’s perspective or recognize knowledge or ignorance in humans, for our purpose it is most important to note that dogs are able to provide humans with information that helps them in obtaining a goal; or, alternatively, dogs can rely on human behavioral cues indicating the lack of certain “knowledge.” Cooper et al. (2003) reported corroborating evidence from an experiment utilizing the well-known Guesser–Knower paradigm (Povinelli et al., 1990). In this study, dogs could not see the hiding process, but could see that a human (the “Knower”) had perceptual access to the hiding. After the hiding both the “Knower” and another human who could not see the hiding (the “Guesser”) appoint one of the hiding places by their behavior and the dog is allowed to choose one of the hiding places (Cooper et al., 2003). Dogs preferred to choose the location indicated by the “Knower,” however, this preference manifested only in the first trial and disappeared later, suggesting that the phenomenon is very elusive.

VIII. CONCLUSIONS

Increasing evidence suggest that wolf–dog–human behavioral comparisons offer a new and fruitful theoretical framework for comparative studies on the evolutionary emergence of social cognition. In this chapter, we argue

for the development of an animal model that not only illustrates a single aspect of human behavior but that is based on a complex level of similarity in a set of functionally shared behavioral features. Our central thesis is that behavioral similarities between the dog and the human represent functional analogies resulting from comparable evolution and development in an environment established and inhabited by humans.

We have argued that three set of skills form the basis for functional behavioral analogies between dogs and humans: (1) the development of social attraction and individualized attachment toward humans and decreased levels of aggression, (2) increased and more flexible means of synchronization (behavioral and emotional synchronization, social learning, and rule following), and (3) complex, prelinguistic forms of communication allowing active information sharing and joint participation in actions. For summary of functionally convergent behavioral features and relevant experimental evidence see [Table I](#).

Note that the wide array social skills allow a very efficient interaction between individuals even in the absence of linguistic abilities. Taking this as an analogy for human sociocognitive evolution, we suggest that early, prehistoric human groups could have engaged in very complex cooperative interactions even if they did not possess the advantages of having a language. From this it follows that the operation of the Dog Behavior Complex has the potential to reflect that early stage of hominid evolution when people facing the need for interaction had to evolve a set of social skills which provided the basis for complex interaction.

The value of this comparative modeling will depend on the degree to which the counterparts of the Human Behavior Complex can be experimentally tested and evaluated in the dog. We think that the theoretical and experimental analysis of Dog Behavior Complex in comparison with the Human Behavior Complex has the potential to provide novel answers to the question of “What makes us human?” future research should extend this approach by making more detailed investigations concerning the convergent aspects of social competence in dogs and humans and the limitations of using the dog as a model species.

IX. SUMMARY

The traditional approach for studying the evolutionary emergence of human social cognition is based on comparisons with apes and monkeys as model species with a homologous relationship to other primates and

humans. Recently, however, research interest has focused on other species offering analogous models for the evolution of human social cognitive abilities. Here, we propose that convergent social evolution in dogs can be used to model the early state of human social evolution suggesting that functionally analogous forms of many traits of the Human Behavior Complex are present in dogs.

We argue that the dog as a model species is unique among domesticated species due to its special domestication history including adaptive specialization as well as developmental socialization of dogs in the human environment. Moreover the dog represents a natural experimental model for studying human behavior because (1) socialization to humans is a natural process in dogs, (2) the dog has a living ancestor, the wolf, and (3) comparison with the ancestor is important for convergent modeling.

Having argued the working hypothesis regarding the dog as a model species in studying functionally analogous behaviors of the human complex, we propose the following program of systematic data collection. First, one defines the elements of the Dog Behavior Complex as discrete, functionally separated components and selects a single component for extensive comparisons (Section V.A). Then one investigates intra- and interspecific comparisons of functionally corresponding behaviors between dogs and wolves (Sections V.B and V.C), and one makes direct comparisons of dogs and humans in functionally similar situations (Section V.D). Finally, a comprehensive approach cannot be complete without comparisons of underlying controlling factors at the behavioral, physiological, and genetic levels (Section V.E).

The experimental evidence so far available reveals some apparent, functional similarities between the human and Dog Behavior Complexes not only at the level of main dimensions (sociality, synchronization, and construction) but at the level of the components. Nevertheless, apart from a few exceptions (e.g., attachment) our present knowledge regarding the components of the Dog Behavior Complex, in comparison with the corresponding skills/traits in wolves and humans, is insufficient.

Therefore, the theoretical and practical significance and the predictive value of the dog model in understanding the evolution of human social cognition stands or falls with systematic experimentation subject to the conditions of this paradigm. We believe that further systematic comparisons involving many aspects of the Dog Behavior Complex will allow modeling of interaction between various components of the Human Behavior Complex, in contrast to other models which are mostly restricted only to a single aspect of human social cognitive skills.

Acknowledgments

The research reviewed here was the outcome of a long-term project supported by various organizations and would not have been possible without the help of the many hundreds of dog owners and the active contribution of their dogs. We are also grateful to students taking part in socializing the wolves. We thank the support of the Bolyai Foundation of the Hungarian Academy of Sciences, Hungarian Science Foundation (T049692), the European Union (FP6 NEST 012787), the charity Dogs for Humans and Horatius Ltd. We are grateful for the comments of Csaba Pléh, Daniel Mills, Paul Bloom, Colin Allen, Tim Roper, and two anonymous reviewers on an earlier version of this manuscript. We would like to express our gratitude to Bea Belényi, Borbála Györi, Anita Kurys, Gabriella Lakatos, Richárd Mányik, Csaba Molnár, Dorottya Újfaluşy, Dóra Újváry, and Judit Vas.

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