REVIEW

Comparative social cognition: what can dogs teach us?

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Research in comparative social cognition addresses how challenges of social living have formed the cognitive structures that control behaviours involved in communication, social learning and social understanding. In contrast to the traditional psychological approach, recent investigations take both evolutionary and functional questions into account, but the main emphasis is still on the mechanisms of behaviour. Although in traditional research 'comparative' meant mainly comparisons between humans and other primates, ethological influences have led to a broadening of the spectrum of species under study. In this review, we evaluated how the study of dogs broadens our understanding of comparative social cognition. In the early days of ethology, dogs enjoyed considerable interest from ethologists, but during the last 20 years, dogs have rarely been studied by ethological methods. Through a complex evolutionary process, dogs became adapted for living in human society; therefore, the human environment and social setting now represents a natural ecological niche for this species. We have evidence that dogs have been selected for adaptations to human social life, and that these adaptations have led to marked changes in their communicative, social, cooperative and attachment behaviours towards humans. Until now, the study of dogs was hindered by the view that they represent an 'artificial' species, but by accepting that dogs are adapted to their niche, as are other 'natural' species, comparative investigations can be put into new light.

Depending on the ecology of the species, individuals interact at variable frequency with conspecifics. Especially for individuals living in groups, companions represent an integral part of their immediate environment. Researchers on social cognition are interested in understanding behavioural processes related to interactions between conspecifics ('social agents'), a topic that is partially based on the assumption, not shared by all researchers, that the mechanisms controlling such interactions differ from those that are at work when the individual interacts with the physical environment. This distinction has been underlined in many pioneering studies on social cognition by ethologists who realized that the social dimension ('social field'; Kummer 1982) of life often presents different challenges for the animal than do physical aspects of the environment (e.g. Jolly 1966; Goodall 1986; de Waal 1986, 1991; Cheney & Seyfarth 1990; Tomasello & Call 1997). Accordingly, we prefer a broad definition of

social cognition that integrates a wide range of social phenomena, including recognition and categorization of conspecifics (e.g. Dittrich 1990) and their emotions (Andrew 1962), the development and management of social relationships ('attachment' (e.g. Wickler 1976), 'friendship' (de Waal 1991)), the acquisition of novel skills by interacting with conspecifics ('social learning'; e.g. Whiten & Ham 1992; Miklósi 1999; Byrne 2002), the manipulation of others by means of communicative signals (e.g. Hauser & Nelson 1991; Gomez 1996), the competence to perform joint cooperative actions and the question of 'mind-reading' skills (e.g. Whiten & Byrne 1991). Furthermore, the study of social cognition should aim to describe mental representations that emerge in the course of social interactions and how these representations affect and control behaviour. However, researchers should not forget Tinbergen's (1963) 'four questions' and should frame their questions in a functional (ecological) and evolutionary context, even if they are more interested in the study of mechanisms and development of behaviour.

In the following review, we argue first that the research agenda of social cognition could be fulfilled only if we expand the number of species under study based on a proper comparative methodology. Second, we present a

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case of this comparative method by introducing the domestic dog as a model species for studying animal (including human) social cognition.

BROADENING THE SPECTRUM: CAVEATS OF COMPARING SPECIES

Traditionally, comparative researchers were interested mainly in the evolution of human social cognition. This approach has concentrated on the study of apes and monkeys ('chimpocentrism'; Beck 1982). Research associated mainly with traditions of comparative psychology has overshadowed the development of an ethologically oriented approach to social cognition for many years. A slow change in behavioural ecology, which has recognized the importance of studying behavioural mechanisms (reviews in Dukas 1996; Shettleworth 1998), has given way to the rediscovery of the importance of investigating social cognitive processes in a functional and evolutionary framework.

There is a huge interest among both psychologists and ethologists in studying social cognition in many species. The traditional 'chimpocentrism' has diminished, and the range of species under study has grown extensively. There is increased interest in relating cognitive aspects of social life to evolutionary and ecological history or constraints of the species under study. Mammals and birds still dominate the field, but investigations in fish (e.g. review in Bshary et al. 2002) and invertebrates (e.g. Fiorito & Scotto 1992) also provide insight into the interaction between social cognition and environment.

However, this diversity of species investigated could add to our scientific knowledge only if researchers understand the limits of the methods used. Several methods have been used in the study of social cognition, and there is a consensus among most researchers that only multiple strategies have the promise to give functional and mechanistic explanations of social cognitive behaviour.

Two lines of approach can be distinguished. The anthropocentric approach relies on investigating the presence or absence of human behaviours in animals in simplified modelled tasks, often looking for simpler so-called 'animal models' (Kamil 1998). Although often criticized, if used with care this research strategy can reveal abilities in animals that would otherwise have escaped our attention. To show the presence of such skills in particular species, such research relies either on naturalistic observations (e.g. evidence for humanlike imitative behaviour in gorillas, *Gorilla gorilla*, from data on food processing: Byrne 1995; instantaneous descriptive accounts of deceitful behaviour to argue for humanlike cheating in chimpanzees and other primates: Whiten & Byrne 1988), or on experimental evidence (e.g. episodic-like memory in the scrub jay, *Aphelocoma coerulescens*; Clayton & Dickinson 1999). However, such investigations are based on the observation that, in functional terms, both the study species and humans often interact similarly with each other or the environment; that is, researchers try to identify functional analogies of behaviour. We should distinguish between evolutionary arguments of this sort

and comparisons that are based on a general approach to social cognition.

The second approach is concerned with direct experimental comparison of species under investigation. Generally, the null hypothesis for such comparison is that there is no difference between the species (cf. Macphail 1987), so finding difference in performance leads to arguments about the function of a particular skill. The merit of such ecologically valid comparisons has been stressed (Kamil 1998; Shettleworth 1998) but has not been fully acknowledged in the study of social cognition. First, comparative studies should involve bidirectional comparisons, i.e. both homologous species (related by common ancestor) and analogous species (not related by common ancestor but sharing abilities of the species under investigation). For example, the study of food storing as an adaptive skill for dealing with occasional shortages of food in the environment has compared a wide range of bird species in learning tasks associated with behavioural mechanisms underlying the efficient recovery of hidden food. Studies have compared not only closely related species (e.g. food-storing marsh tits, *Parus palustris*, and nonstoring blue tits, *P. caeruleus*; e.g. Healy & Krebs 1992) but also birds from different evolutionary clades (corvids and parids; Clayton & Krebs 1994).

Second, one has to ensure that there are no a priori reasons that one species could not perform the task, because each species is the result of an adaptation process, and investigators have good reason to assume that sensory or motor abilities could interact with the requirements of a specific experimental set-up. Often, species-specific preferences or phobias counteract the performance in experimental tasks, and the species difference obtained in such comparisons is not the result of the behaviour investigated (performance bias). This error can be committed if one compares behaviours of distant species such as between dolphins, apes and humans.

Third, species to be compared must have the same experience both with the environment in general as well as with the particular situation in which the animals will be tested (experience bias). For example, differences in sensitivity to novelty or speed of habituation could lead to false interpretations of cognitive differences between species (Lefebvre 1995). Many ape–human experimental comparisons show experience bias, because the social experience of young children and most captive apes can hardly be compared (see e.g. Povinelli et al. 1997).

Fourth, to exclude the presence of performance and experience biases, researchers should systematically modify experimental variables so that the species assumed to be 'inferior' could also be able to improve its level of performance ('positive control').

Finally, both observations on free-ranging animals and laboratory experiments in the field of social cognition are often restricted to relatively few individuals. This issue of small sample size raises problems of validity in generalizing data to the entire species or using them as arguments in species comparisons. There is a big difference between whether individuals are able to perform a given task and whether this ability is a population/group phenomenon. For example, most available scientific data on apes' ability

to learn aspects of human-type language come from one or at most a few individuals (Savage-Rumbaugh et al. 1993). In contrast, there are few observations on whether individuals of any ape species would use such an ability in the wild, or what kind of species-specific communication system they use. Such an individual ability, which has been shaped by idiosyncratic processes interacting between genetic and environmental influences, may not be a feature of the species. Individual achievements of this sort are important to understand the 'potential' of a species, but on their own they provide little understanding on the evolution of social cognition in that species. Nevertheless, to justify individual-based studies, it has often been argued that, just as general abilities are shared by all members of the species, so individual performance should be based on mechanisms that are potentially available to others (see e.g. Savage-Rumbaugh & Lewin 1994).

CLASSICAL ETHOLOGY AND A NEW ETHOLOGICAL APPROACH TO THE STUDY OF DOGS

By definition, ethology is the study of the behaviour of animals living under natural conditions. Natural conditions can be described as the environment where most members of the species live and reproduce, and have been living for an extended period. Dogs have often been regarded as an ethologically 'uninteresting' species, given their curious history of domestication, even though the dog is one of the most successful mammalian species that has dispersed around the earth. Studies reflecting increased interest in the social behaviour of Canidae in the 1960s and 1970s viewed the dog as a kind of 'control'

species in comparison with 'real', wild canid species such as the wolf, *Canis lupus*, jackal, *C. aureus*, and coyote, *C. lactrans*; e.g. Fox 1971; Bekoff 1977; Frank 1980; Frank & Frank 1982. Perhaps the most well-known study involving dogs was aimed at understanding genetic aspects of social behaviour (Scott & Fuller 1965), but even there the behaviour was described only as a kind of phenotype with little reference to natural behaviour of dogs.

In our view, dogs have to be investigated in their own right. The scientific community is now considering this notion seriously, in that behavioural research on dogs has increased dramatically in recent years (Fig. 1). It has to be recognized that dogs are the product of evolution whichever process has been involved. Domestication can be interpreted as a special form of evolutionary change (by which 'a population of animals becomes adapted to man and to the captive environment by genetic changes'; Price 1984, page 3), but there are other processes, such as the evolution of host–parasite systems or of different forms of symbioses in groups of animal species. Genetic evidence places the emergence of dogs between 35 000 and 100 000 years ago (Vilá et al. 1997; Savolainen et al. 2002), although there is still uncertainty about the timing (for an account of evolutionary processes that could have shaped behaviour of the dog, see Coppinger & Coppinger 2001).

We propose that through an evolutionary process, the dog as a species has moved from the niche of its ancestor (which is shared by wolves) to the human niche, which represents the dog's present natural environment. In this new niche, being a social species, dogs have formed a close contact with humans (at both species and individual levels), which has led to the emergence of heterospecific social groups. It follows that dogs can and should be studied in their natural group, that is, where and when
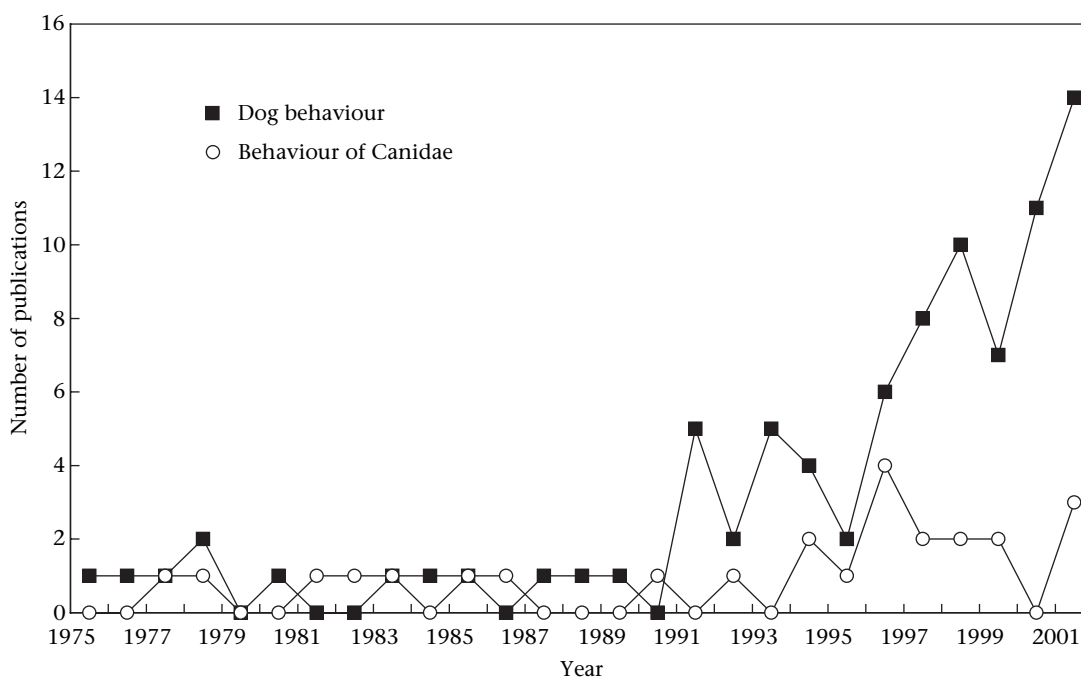
Figure 1. The number of papers aimed at studying behaviour in Canidae, including the dog. (Data were obtained by searching on the Web of Science with the phrase 'dog behavio(u)r'.)

they are living with humans. We have been combining the methods of naturalistic observation and experimentation on heterospecific groups involving dogs and their owners. This approach has turned out to be very useful, not only for the study of dog social cognition, but also for comparative social cognition in general, provoking new questions and perhaps providing some answers to the evolution of social cognitive systems, and in particular to the emergence of complex human social skills.

THE CONTRIBUTION OF DOGS TO UNDERSTANDING SOCIAL COGNITION

As described above, comparative work is an essential part of social cognition research. Dogs can offer the following novel aspects to the study of social cognition in an evolutionary framework. First, the switch of niches by the dog could have been achieved only if it had been accompanied by some forms of behavioural change, at least on the part of the dog (for the present discussion we put aside the issue of changes in the behaviour of humans in relation to the dog). This behavioural change could in part be because the association with humans, who live in more complex social systems than dogs, provided different selective forces. It has often been hypothesized about the evolution of primate intelligence that the increasing complexity of social systems is the driving force for the emergence of sophisticated social skills (Humphrey 1976). Thus, the universality of the social intelligence hypothesis can be tested by assuming that, if true, we should find increased social abilities in domestic dogs. This would mean that, in comparison to their wild counterparts, dogs should have developed novel social skills as a result of adaptation to the human niche. Many aspects of social behaviour would require at least some changes. Living together or in close contact with members of another species presupposes, for example, novel abilities to form individual social relationships ('attachment'), to adopt a flexible communication system for interspecific communication, to recognize the other species as a source of social information (interspecific social learning) and to have the willingness for cooperation. Thus, even if the ancestor of the dog was a highly social species, as is probable, there is reason to suspect that the behavioural changes in dogs were supported by genetic changes. This line of research is aimed at pinpointing those aspects of dog behaviour that make the species adapted to live in the human environment.

Second, such behavioural adaptations in dogs should have produced behaviours that can be regarded as functional analogues of their human counterparts. Many examples show that similar environmental conditions offer the possibility for the evolution of similar behavioural traits (convergence), even in distant species (e.g. Lorenz 1974). The functional aspects of convergent traits are similar, but the underlying mechanisms might differ. Observing and understanding convergent phenomena in evolution is important to evaluate whether the emergence of a trait in another species is a response to an evolutionary challenge and not a product of chance. The study of dogs offers a useful alternative to the study of human traits in the view of evolutionary processes, because dogs could have evolved many such traits as a result of their adaptation process. As we have argued above, the emphasis on comparing human behaviour to homologous traits present or absent in monkeys and apes gives only half of the evolutionary picture; furthermore, our long evolutionary and ecological separation from our nearest relatives could have led to many changes in the epigenetic process that mask similarities that could be traced back to a common ancestor. Therefore, as strange as it may appear, the study of dog social cognition as a collection of functional behavioural analogies, or convergences, increases the chance of understanding the evolution of such abilities in primates, including humans. From a different point of view, Povinelli & Giambrone (1999) have argued that cognitive performances should not be explained by the 'argument by analogy'; that is, because of the close genetic and evolutionary relationship between chimpanzees and humans, the behavioural mechanisms underlying similar behavioural traits are necessarily the same in the two species. Comparative investigations in dogs could highlight that similar social skills can evolve independently, and probably rely on different behavioural mechanisms.

Third, compared with monkeys and apes studied mainly in captivity and under seminatural conditions, dogs, like human children, can be observed in their natural environment. Dogs (and children) are prepared in an evolutionary sense to live in the human environment, but apes, monkeys and other species need to be individually socialized to be available to such comparative research. Furthermore, both dogs and humans have to experience such an environment to develop appropriate species-specific behaviour. In dogs, domestication should be viewed not only as a process that adapted the animal to the human environment, but also as an accumulation of genetic changes that rely on ('expect') certain environmental input and interaction with the environment to exert their full contribution to the emerging behaviour of the individual. Therefore, applying the term 'enculturated' introduced to account for more humanlike social skills in chimpanzees reared in close human contact in households (e.g. Tomasello & Call 1997), we should distinguish between species that can be enculturated by rearing such individuals in a human environment, and species that are enculturated as part of their natural development. Furthermore, the similar enculturation process of dogs and children allows for the design of comparative studies that are based on the same methods and procedures.

Fourth, dogs represent not only a species but also a set of very variable populations that differ in their genetic bases (breeds) and levels of socialization (e.g. feral dogs, dogs living in shelters, working dogs). Over many hundreds of years, dogs have been selected for different abilities in their interactions with humans. For example, at the behavioural level, Coppinger & Coppinger (2001) discriminated between sled dogs, livestock-guarding dogs and herding dogs as selected to perform different tasks. However, the dog's type of work also determines its type of interaction with humans. The question here is whether and how such genetic diversity influences social cognition

in dogs, and whether there are social abilities shared by all dog breeds independent of their genetic makeup. Equally important would be to know the role of the social environment in shaping social abilities of dogs, by comparing dogs that have been reared in different human environments at different levels of social interaction with humans. In the study of complex social skills, dogs present one of the few possibilities where limited experimental manipulation on many individuals is possible, and such research should shed light on how genetically derived information interacts with the social environment.

SOCIAL RELATIONSHIPS AND THEIR EFFECTS ON SOLVING PROBLEMS

For animals living in long-term social groups, the relationship to others provides the framework for everyday life. This has long been known by primatologists who investigated both interindividual relationships and relationships between classes of group members (e.g. de Waal 1991). Theories based on arguments of kinship or investment can explain the functional reasons for these social structures, but they do not explain the mechanisms underlying interindividual associations.

For example, until recently there has been little research on dog–human social relationships. Psychological questionnaire-based investigations have documented that humans form close attachments to their dogs, but the issue has not been investigated by using behavioural observations at the group level (e.g. Barker & Barker 1988; Serpell 1996). Ethologically inspired research on human attachment (Bowlby 1969; Scott 1992) led to the development of a test that has been used successfully to demonstrate features of attachment behaviour in humans, particularly between mothers and their infants (e.g. Ainsworth & Wittig 1969). An application of the same test to dogs and their owners provided analogous results (Topál et al. 1998). As in the human research, researchers including ourselves have been able to identify patterns of attachment relationship that closely match the categories described for human mothers and their infants. This result suggests that variability in the types of relationships found in humans is also present in dogs. This variability seems to depend less on breed-specific genetic differences, because the same variation was also found within a breed (e.g. Gácsi et al. 2001; Gácsi 2003).

Traditionally, problem-solving ability has been investigated by testing a single individual isolated from its groupmates. So at first sight, the issues of social relationship and problem solving do not seem to be related, but a closer investigation reveals that, in animals living in close contact with group members, many individual actions can be affected by the presence and actions of others. Thus, for a social animal, there is one alternative to solving a problem on its own and another by capitalizing on skillful companions to solve the problem for it (a similar argument could be made at the individual level for the producer–scrounger relationship). In experiments on problem solving in group-living chimpanzees, the dominant chimpanzee did not need to learn the solution of the task. An equally successful alternative strategy was to take away the food after the subordinate got his reward by solving the problem (Chalmeau & Gallo 1993). A similar strategy is often used by human infants to manipulate their social environment to achieve their aims (social tool use), and similar behavioural observations have been reported in a socialized gorilla infant (Gomez 1990). Apparently dogs are also able to use alternative strategies in solving problems, and this seems to depend partially on their relationship with the human caretaker. Dogs living in the garden solved a food-getting problem faster than dogs living in flats in the presence of their caretaker (Topál et al. 1997). However, this difference was not attributable to differential experience or other possible environmental factors, because the dogs living in the flat solved the problem equally well after the caretakers gave them verbal encouragement. The behavioural analysis of the dogs living in flats showed that, when faced with a novel problem, they first looked at the caretakers. Given that later they were able to solve the problem on their own, one interpretation is that they first used an alternative, social strategy of waiting for the owner to solve the problem for them. This early observation gained further support when we compared the behaviour of highly socialized young wolves and dogs in a similar situation (Miklósi et al. 2003). In one task, subjects were trained to pull out a rope with a piece of meat attached at its end from a cage. After acquisition, which did not reveal species differences, the rope was fastened to the bars of the cage (invisibly for the subjects), and the animals were allowed to try to get the meat. Although most members of both species started to pull the rope, dogs started to look at the human, present behind them, much sooner and for longer than did their wild counterparts. Given that all subjects were reared in similar social environments, genetic differences in the tendency to look at human faces could be responsible (Miklósi et al. 2003).

This result suggests that investigations on problem-solving ability in a social context should consider the effect of other group members on the performance of the individual under study. For example, the inferior problem-solving performance of dogs in comparison with wolves reported by Frank (1980) might have been partly the result of the alternative social strategies used and not necessarily the cognitive constraints on the species.

## COMPARATIVE ASPECTS OF COMMUNICATION

Social groups are often characterized by intensive multi-channelled communication behaviours that enmesh many aspects of everyday life. Although animals live in different environments, their communicative behaviour can be viewed as a kind of control system that allows group members to synchronize activities (Csányi 2000). In general, the production of communicative signals strongly depends on the motivational state of the sender, is composed mainly of species-specific actions and is correlated with the context (e.g. Smith 1977; Owren & Rendall 1997). A challenge is whether and to what extent animals might use signals that bear some reference to external

environmental events (Evans 1997) and are independent of the motivational state and context (Marler et al. 1992). In a functional sense, the warning of group members on attacking predators would provide such an example. Research in many potential prey species has identified such communicative systems where signals seem to have referential character (review in Evans 1997). However, close inspection of alarm communication in most of these species reveals only a limited flexibility in the use of these signals, and only a few cases where such signals are used outside their original context (e.g. to frighten off competitors when no predators are present; Møller 1988).

Seminatural observations on chimpanzees showed that they use many signals with communicative intent relatively flexibly (e.g. Tomasello et al. 1989), which is paralleled by observations on chimpanzees living in human social environments (e.g. Savage-Rumbaugh et al. 1993; Leavens et al. 1996). Close investigation of chimpanzee–human gestural communication, however, reveals some anomalies. Chimpanzees apparently have problems relying on the human pointing gesture as a signal for environmental events. In experimental two-choice situations where the presence of hidden food (in one of two potential hiding places) is signalled by pointing, chimpanzees showed low levels of performance (e.g. Povinelli et al. 1997; Itakura et al. 1999), despite their natural ability to use gestural signals. Comparative experiments provide evidence that dogs perform very well at using the pointing gesture for finding food (Fig. 2a; e.g. Miklósi et al. 1998; Hare & Tomasello 1999; McKinley & Sambrook 2000). Furthermore, dogs are able to generalize to novel forms of the pointing gesture, suggesting some level of understanding about the referential character of the signal (Soproni et al. 2002). A further difference between chimpanzees and dogs is that, by using the pointing gesture, dogs could be directed to a container hiding food, even if the human stood near the other, empty container (Fig. 2b). These observations suggest that dogs use human gestural signals flexibly and adaptively.

One could argue that, having been reared in close human contact, dogs in these studies might have simply learned the gesture associatively, even if the chimpanzees in the comparable studies also had immense experience with humans. To tackle this problem, members of our
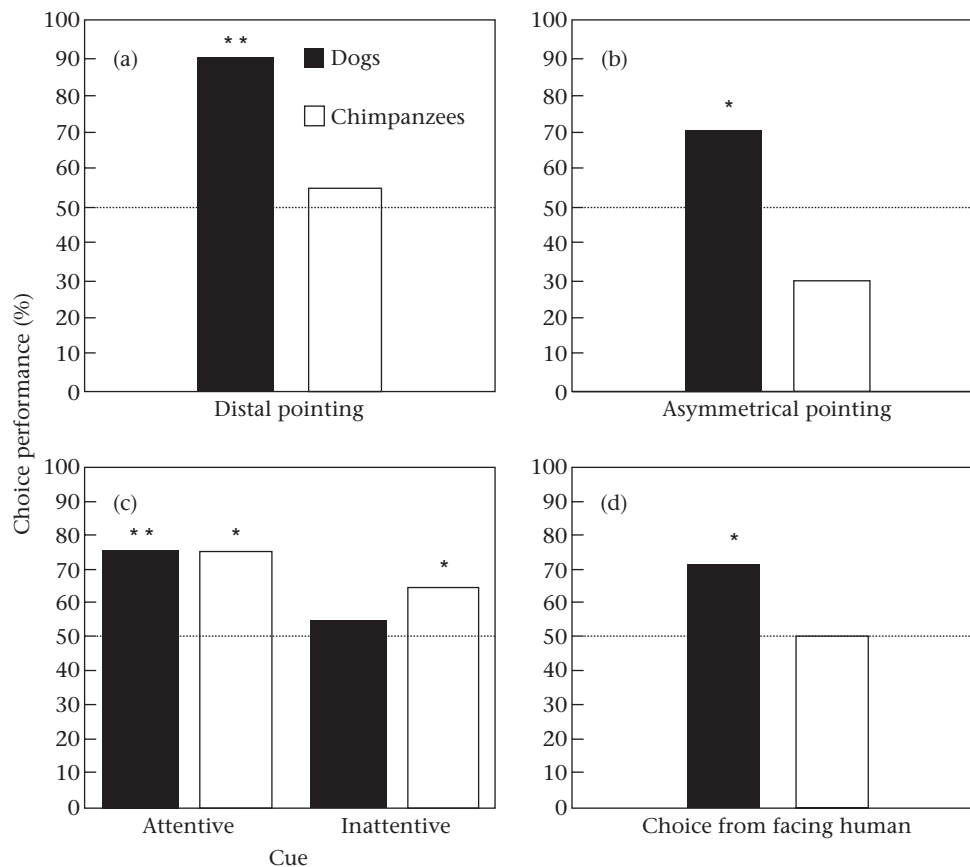
Figure 2. Comparison of studies of dog and chimpanzee performance in communicative situations with humans. (a) Choice performance in response to 'distal pointing gestures' (experimenter's index finger is about 50 cm from the location of food (chimpanzees: Povinelli et al. 1997, $N=7$; dogs: Soproni et al. 2002, $N=9$)). (b) Choice performance when the experimenter stood next to an empty hiding place and pointed to the opposite one, containing food (chimpanzees: Povinelli et al. 1997, $N=7$; dogs: Soproni et al. 2002, $N=9$). (c) Choice performance when the correct place was signalled by looking at it ('attentive cue') or the experimenter looked at the ceiling above the location of the hidden food ('inattentive cue'; chimpanzees: Povinelli et al. 1999, $N=7$; dogs: Soproni et al. 2001, $N=14$). (d) Choice performance in a begging situation when subjects had to choose between a facing and a nonfacing human with the body torso orienting forward (chimpanzees: Povinelli & Eddy 1996, $N=7$; dogs: Gácsi et al., in press, $N=19$). All significance levels (*$P<0.05$; **$P<0.01$) as indicated by the original authors.

research group reared four wolf puppies in close human contact. After extensive training, only one animal achieved comparable levels of responding to the pointing gestures, although the testing was done under identical conditions as with dogs, and wolves seemed to use other human-provided visual signals (e.g. touching) as cues for the location of food (Miklósi et al. 2003). This comparison between dog and wolf behaviour suggests that dogs have a genetically based advantage in understanding the human pointing gesture (see also Hare et al. 2002). Given similar abilities reported for dolphins, *Tursiops truncatus* (Herman et al. 1999; Tschudin et al. 2001), one could assume that different social selection pressures led to the emergence of this behaviour.

Results from observing chimpanzees outwit each other in competitive situations could provide an explanation (Hare et al. 2000). In these tests, chimpanzees apparently could perceive and forecast the behaviour of another on the basis of realizing what the other had or had not seen. Submissive animals preferentially chose hidden food items that the dominant animal had not seen hidden. This result suggests that chimpanzees were much more successful in a competitive situation with a conspecific than in a cooperative situation with a human. The two-choice situation requires cooperative interaction between the participants, so this conclusion could explain the inferior performance of chimpanzees compared to dogs (Hare & Tomasello 2004). Domestication may have promoted further social skills in dogs, which allowed the development of complex cooperative social interaction, which might in turn also provide the basis for training dogs to assist blind or mobility-disabled people (e.g. Naderi et al. 2001).

Observational studies have also established that dogs rely on various signals to direct the attention of a human to places of interest. Based on the signals provided by dogs, experimentally naïve owners were able to find a piece of hidden food (Miklósi et al. 2000). To achieve the animal's aim, such behaviour consists of two elements. The signaller needs to direct the attention of the other simultaneously to itself and to the location in the environment. Dogs achieve this by looking at the owner or vocalizing (attention-getting signals) and looking at the place of hidden food. Observing the pattern of such ostensible communicative behaviour in dogs suggests close functional parallels with human infants (as well as with a gorilla; Gomez 1996), because both dogs and humans rely on vocal signals and use directional looking and gaze alternation to communicate the location of food.

Recognizing attention influences many aspects of communication, so it is not surprising that there is a species difference between chimpanzees and dogs in the recognition of human attention. According to our observations, dogs use signals of human attention to direct their behaviour in a choice situation (Soproni et al. 2001). Looking into a baited container signalled the presence of food for the dogs, but looking above the container did not (Fig. 2c). This was not true for chimpanzees, who did not take such cues into account before making their choice and in both cases chose the 'signalled' container (Povinelli et al. 1999). This difference in recognition of human attention gained

further support when it was shown that dogs were able to use face cues to decide from which person to beg food. In comparable experimental situations, both dogs (Gácsi et al., in press) and chimpanzees (Povinelli & Eddy 1996) were offered the opportunity to beg food from two persons, one who faced the subject and one that looked in the opposite direction (the orientation of the torso was the same for both). Dogs but not chimpanzees selectively begged from the person facing them (Fig. 2d). The explanation for this difference between chimpanzees and dogs is not clear. One possibility is that chimpanzees have species-specific constraints that counteract learning about human-specific cues of attention. If, for example, chimpanzees regard body orientation as a species-specific cue for attention (which, in natural situations, is highly correlated with looking direction), then they could ignore or be less sensitive to experimental manipulations that separate the two cues. We have seen that, compared with wolves, dogs show a clear preference for following a human gaze (Miklósi et al. 2003), so they could be 'preadapted' to learn about the significance of gazing in humans.

SOCIAL LEARNING IN A HETEROSPECIFIC RELATIONSHIP

Earlier studies of social learning in dogs (Adler & Adler 1977; Slabbert & Rasa 1997) were concerned mainly with within-species learning. However, dogs are often separated from their mother at a relatively early age, so they have only a limited possibility to learn from conspecifics. Again, the ethological question is whether dogs are able to learn from their heterospecific companions. In a series of experiments, we found evidence that dogs use socially provided information to solve problems in a barrier task (Pongrácz et al. 2001) or to learn how to manipulate simple machinery (Kubinyi et al. 2003). For example, dogs that could witness a human demonstrating a detour around a fence were much faster at acquiring the detouring behaviour than were nonobserver (control) dogs. Although such observations represent an important starting point in natural situations, social learning does not take place in isolation, but interacts with other forms of individual experience (e.g. Galef & Whiskin 2001). Therefore, one question is how flexible dogs are at using socially provided information. In a version of the barrier tasks, a group of dogs was given the opportunity to reach the goal object through an opening in the fence. Dogs without the possibility of observing humans detouring around the fence could not solve the problem after the opening was closed. These dogs continued to try to get through the closed opening, but observer dogs rapidly adopted the detouring strategy shown by a human demonstrator (Pongrácz et al. 2003). Furthermore, socially acquired habits sometimes seem to exert marked effects on the behaviour of dogs, in that dogs seem to rely on such habits even if the habits become maladaptive in a novel situation (Pongrácz et al. 2003).

Experimental evidence about many forms of social learning in dogs shows that dogs generally achieve the complexity and flexibility present in monkeys (marmosets, *Callithrix jacchus*: Bugnyar & Huber 1997), apes (e.g.

chimpanzees; Whiten et al. 1996) and many other mammalian species. The unique aspect of dogs' performance is that it takes place in a heterospecific relationship. Learning from a member of another species is not rare in birds (e.g. Sasvári 1979) or between chimpanzees and humans (e.g. Custance et al. 1995), but learning from another species with such a dissimilar morphology is worth further investigation. For example, in a recent study, dogs observed that pushing a handle by hand resulted in a ball rolling out (Kubinyi et al. 2003). Most dogs used their nose to touch the handle instead of the foreleg, which is homologous to the human arm, suggesting that in this situation the dog's goal was to move the handle and not to replicate the human action.

THE BEGINNING OF AN ADVENTURE

The studies presented here should be regarded as only a first step in understanding social cognition in dogs. The limited space offered comparison mainly with only one other species, the chimpanzee, for which the most comprehensive knowledge of social cognition in nonhumans is available. There is further need to investigate other species, as it is already happening in dolphins (Herman et al. 1999) and social birds (e.g. Pepperberg 1991; Fritz & Kotrschal 1999; Emery & Clayton 2001) to put the social cognition of the dog in broader perspective. Dogs provide ample evidence for behavioural flexibility across many social situations involving communication and social learning. Many behavioural features in dogs have been identified that could be functional analogues of human behaviour. It would be interesting to explore the extent to which dogs depend on human social environment for the development of social skills. However, it remains to be seen whether the apparent complexity of analogous behaviours in dogs to humans is paralleled by the emergence of more complex representations, as seems to be the case in our species. Finally, if we have the challenge to understand the mind of another species, why should we not choose our best friend for this endeavour?

Acknowledgments

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