Comparative social cognition: The dog as a model for understanding human social behaviour

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SUMMARY

Most evolutionary models of human behaviour are looking for sine qua non of being human. Such single-factorial approaches target usually more general (i.e., linguistic ability) or more specific cognitive skills (i.e., shared intentionality), or present a causal chain of skill evolution in humans. Csányi (2000) proposed an alternative analysis suggesting that, after the Pan-Homo split, human behaviour evolution underwent a series of small changes affecting a wide array of social features. The so-called "Human Behaviour Complex" provides a framework for those skills in which these changes were the most significant. The basic statement of this model is that human behavioural evolution should not be explained by a single causal chain of changes but, instead, it is the result of a "mosaic evolution" of several skills that gave rise to complex social behaviour in a synergetic way. This multifactorial approach identifies three important general behavioural dimensions (sociality, behavioural synchronization, constructive skills) that affect most social skills to some extent, and assumes that it is the sum change in these dimensions of behaviour, which, on the surface, produce a qualitative difference, in comparison to our closest relatives. It is assumed that this behavioural evolutionary process was governed by newly emerging environmental challenges for the Homo species including the social dimension of their lives.

The general aim of this dissertation is to provide a conceptual and theoretical framework as well as empirical findings for the notion that functionally analogous forms of many traits of the Human Behaviour Complex are present in dogs and therefore domestic dog (Canis lupus familiaris) represents a natural experimental model for studying some aspects of the human behaviour in general and human social-communicative skills in more particular. The first part of the dissertation (chapters 1 & 2) is devoted to arguing that comparative social cognition provides a comprehensive framework for understanding the evolutionary origins of uniquely human social skills as well as to outlining the idea that "caninization" (i.e. the evolutionary process that led to the emergence of domestic dog from the wolf), and hominization can be seen as convergent evolution during which functionally humananalogue behaviours emerged in dogs. This approach is based on the argument that after having been adapted to similar environments different species might develop functionally similar skills. Accordingly, we may assume that dog-human and dogwolf comparisons make us possible to understand how adaptational challenges by the human social environment could lead to the emergence of social cognitive abilities in dogs. The second part (chapters 3-5) includes several experimental studies that have been conducted over the past few years with the aim of providing empirical support for this theoretical framework. These experiments focused on different aspects of dogs' social cognition including (I) social attraction and attachment in interspecific (i.e. dog-human) relationships; (II) increased and more flexible means of synchronization (behavioural and emotional synchronization, social learning and rule following); and (3) complex, pre-linguistic forms of communication allowing active information sharing and joint participation in actions. Finally (chapter 6) we review the different approaches to characterization of dogs' social competence and provide a synergetic model of the emergence of socio-cognitive skills in dogs. We also provide a description of the infant-like functional aspects of dogs' social cognition and show how these functionally human-analogue manifestations of social-cognitive skills make the dog able to participate in communicative interactions in a preverbal infantlike manner.

PART I.

INTRODUCTION AND THEORETICAL FRAMEWORK*

It is widely agreed that one of the important and controversial questions for cognitive science is "What makes human behaviour and cognition unique in the animal kingdom?" From an empirical viewpoint, not denying the generally accepted premise that the evolution of human behaviour 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 behaviour.

In searching for answers to these questions, different disciplines argue for different approaches suggesting theoretical and/or experimental analyses of human behavioural 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 behaviour. Comparative social cognition looks for the presence or absence of human-like skills in animals that are often directly comparable at the behavioural level and suggests that the issue of human uniqueness can be addressed by asking about the specific behaviours of our species with respect to cognitive functioning. Here we argue for the utilization of the domestic dog as a model organism that not only illustrates a single aspect of human behaviour but there is a complex level of similarity in a set of functionally shared behavioural features.

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CHAPTER 1

AN INTRODUCTION TO THE ISSUE

1.1 WHAT MAKES US DIFFERENT FROM NON-HUMAN SPECIES? THE HUMAN BEHAVIOUR COMPLEX

While searching for the "crucial difference" between human and non-human behaviour and the underlying cognitive mechanisms, many researchers have focused on a single causal chain of events involving the effect of environmental factors and adaptive behavioural 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, Kruger and Ratner (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 and his colleagues (2005) have argued that the crucial difference between human and non-human 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 identificationbased imitative learning (Tomasello et al. 2003a), or the evolution of the ability to teach and to learn from teaching (pedagogical receptivity – Csibra & Gergely 2009). 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 & 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 withingroup interactions have been increasingly influenced by cooperative tendencies (Hare & 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 (Povinelli et al. 1990; Hare et al. 2000). The fact that apes usually under-perform in cooperative tasks suggests that their social competence is biased toward competitive situations (Hare, 2001). In line with this assumption some experiments seem to provide evidence that apes (Melis et al. 2006), unlike humans (Warneken and Tomasello 2007), show limitations in cooperation.

A common feature of the aforementioned approaches to human behaviour evolution is that all of these lay emphasis on a single "main" cognitive feature. Others, however, argued against these 'unidimensional', 'sequential' approaches because it is unlikely that the separate effect of a single or a few behavioural features determined human evolution (see e.g. Csányi 2000). The aforementioned approaches can be contrasted with system theoretical models (Csányi 1989) emphasizing the parallel nature of changes that have taken place in the process of human behavioural evolution. That is, instead of assuming major dramatic alterations, hominization can be viewed as a series of successive and parallel small changes in a wide set of skills,

as a process that affected many features of human behaviour in a complex interacting way (Byrne 2005; Hermann et al. 2007).

Nowadays, it is increasingly accepted that parallel emergence of some behavioural alterations and their simultaneous presence might provide a more plausible hypothesis for human-specific behaviour. Csányi (2000), for example, has proposed that during evolution, humans adopted a set of species-specific skills that influenced critically their social life, allowing them, among others, to form large, closed individual groups. These include advanced cognitive skills as well as other behavioural traits which have evidently played a role in the manifestation of human-specific cognitive skills.

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

The first one, sociality, refers to those components of social behaviour that contributed to marked changes in sociality. After socialisation, 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 towards strange groups (xenophobia; LeVine & 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).

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 behavioural mimicry ("blind" imitation), and activities involving teaching (Csibra & Gergely 2009) and other disciplining behaviours. The spontaneous human tendency to follow social rules (de Waal 1996) is especially advantageous in organizing the behaviour 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 are able in general 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 over-hearing linguistic interactions.

The third group of traits is concerned with the constructive character of social behaviour. In contrast to animal communication systems that transmit mainly the inner motivational state of the signaller, 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 non-human species (Bickerton 1990). Humans are not exceptional among animals in using tools, although non-human 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 towards themselves, so as a result, the group continuously reconstructs itself over time (Csányi 1989).

In summary, it seems that the success of present day Homo sapiens lies in the fact that it has accumulated a very efficient set of these abilities which led to the emergence of complex human-specific social skills. The empirical answer to the question of human uniqueness is, however, complex because behavioural traits and their underlying cognitive mechanisms develop as a result of epigenetic processes consisting of interactions between the social and non-social environment and the genetic makeup of the organism. In searching for answers to these questions, different disciplines argue for different approaches suggesting theoretical and/or experimental analyses of human behavioural evolution and its underlying cognitive processes.

1.2. COMPARATIVE SOCIAL COGNITION: A COMPREHENSIVE FRAMEWORK FOR PRACTISE AND THEORY

Comparative studies have a long history in experimental psychology. Sometimes the subject in question serves as a model for some particular ability or their ability is evaluated in relation to some supposed human performance (see Kamil 1998 for an overview). It is important to note, however, that in modern life sciences one has difficulties to formulate questions without taking evolutionary models into account, and behaviour (including its social-cognitive aspects) is not an exception. Although in early research on comparative cognition a clear evolutionary argument was often hard to find, later investigations have changed the state of affairs providing a rich theoretical framework for understanding how social cognition might have emerged and changed in the course of evolution (see Shettleworth 1998 for a review).

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, 1991a; Cheney & Seyfarth 1990; Tomasello & Call 1997). Broadly defined, social cognition 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 1991a), the acquisition of novel skills by interacting with conspecifics ("social learning" - e.g. Whiten & Ham 1992; Miklósi 1999; Bates & Byrne 2010), the manipulation of others by means of communicative signals (e.g. Hauser & Nelson 1991; Gomez 1996a), the competence to perform joint cooperative actions and the question of "mind-reading" skills (e.g. Whiten & Byrne 1991). Furthermore, social cognition research often aims to describe mental representations that emerge in the course of social interactions and how these representations affect and control behaviour (see e.g., Smith & Collins 2009).

In recent years there have been several interesting shifts in research tendencies in the field of comparative social cognition. Perhaps most important, scientists moved out from the somewhat cryptic corners of their laboratories and have begun to study their subjects in the field. This change stems from the recognition, that comparative studies can be (and should be) put in a broader perspective. Based on the seminal paper by Tinbergen (1963) it was increasingly accepted that in line with his "four questions" one should frame research questions in a functional (ecological) and evolutionary context, even if the study is aimed at the mechanisms and the development of the behaviour. This move gained support from behaviour ecology research because of the increasing interest in behaviour mechanisms behind the functional considerations of behaviour. Behavioural ecology has recognized the importance of studying behavioural mechanisms (reviews in Dukas 1996; Shettleworth 1998) and this has given way to the rediscovery of the importance of investigating social cognitive processes in a functional and evolutionary framework. Although the research field of comparative cognition associated mainly with traditions of comparative psychology, in line with these changes, cognitive ecology (Healy & Braithwaite 2000) has emerged as a new integrative research field that attempts to integrate functional explanations of behaviour with an understanding of the cognitive mechanisms.

A further shift is attributable to the new challenges of social cognition sparked by influential volumes on Machiavellian intelligence and more broadly on the evolution of social cognition including the problem of theory of mind (e.g., Byrne & Whiten 1988). Experimental work on social cognition involved much richer procedures, which drifted away from the relatively inflexible systems investigating associative learning by Pavlovian or Skinnerian methods. Traditionally, comparative researchers were interested mainly in the evolution of human social cognition and have concentrated on the study of apes and monkeys ("chimpocentrism" - Beck 1982). However, in line with the increasing acceptance of evolutionary viewpoint, nowadays it is widely accepted that a modern research agenda in comparative cognition cannot be restricted to only a handful of species. This slow change has been preceded by intensive discussions on whether such a move would be useful or actually unproductive. Supporters of the latter arguments insisted that there have been only a few significant transmissions in the evolution of animal cognition; therefore, for studying cognitive architecture, only a few "flagship" species are needed. In contrast, others have argued that the phylogenetic considerations should be taken more seriously (Shettleworth, 1998), and instead of hypothesizing prematurely some sort of cognitive ladder in the evolution of animals, a detailed analysis could lead to much

better understanding of how ultimate causes like evolutionary history and local adaptation might have been supported by changes in mental mechanisms.

The traditional "chimpocentrism" has gradually diminished, and current 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 across a wide range of human and non-human animal species (Emery & Clayton 2009).

1.3 TRACING THE EVOLUTIONARY ORIGINS OF UNIQUELY HUMAN SKILLS

1.3.1. On the hunt for the homologous traits

At present, comparative social cognition is widely believed to be the most relevant discipline to deepen our understanding of the evolutionary origins of human behaviour. Comparative social cognition looks for the presence or absence of humanlike skills in animals that are often directly comparable at the behavioural level and suggests that the issue of human uniqueness can be addressed by asking about the specific behaviours of our species with respect to cognitive functioning. When it came to the comparative aspects of human cognition, primates always had an exceptional role (Povinelli et al. 1999). The scientific interest in primates, and especially in apes, gained power after it became undeniable that humans and apes shared common ancestors in some distant past, six million years ago. Köhler (1925) and Yerkes (1930) were among the first influential scientists who took this challenge seriously, and studied the cognitive abilities of monkeys, and especially apes, in detail. Researchers felt an urge to look for similarities between humans and apes, and a long battle began between proponents of evolutionary continuity seeing only quantitative differences and those, who suggested that there are major qualitative differences. Perhaps the most exposed case was the comparative study of language use in apes where both type of arguments have often been referred to (Savage Rumbaugh et al. 1993; Wallman 1992). With some breaks of variable duration, this tradition has continued until today and includes research laboratories all over the world and in many field stations in the natural habitats of these species (for a monograph see Tomasello & Call 1997).

This trend in comparative cognition has mainly been concerned with homologies in behavioural or cognitive skills. Such research programs are centred around the problem of whether the origin of some behavioural traits or cognitive skills can be traced back in time, i.e., whether they can be assumed to have been present in the common ancestor or, alternatively, whether they have evolved after the Pan-Homo split and thus are possibly adaptive (but see Gould & Vbra 1982) species-specific traits in Homo sapiens. In line with the notion that any similarity in certain abilities could be interpreted as a feature that existed already in the common ancestor, comparative work has revealed an array of social behavioural traits which appear to have a common origin in Homo and apes (e.g., de Waal 1996).

Many studies, however, reported specific differences between humans and other great apes (e.g., Povinelli et al. 1999). These findings are of great importance because they call for specific hypotheses about the selective nature of ecological and social environments that has provided the evolutionary scenario(s) since our lineage split from the other great apes (Hermann et al. 2007). In fact chimpanzees and

humans not only are separated by 6 million years of evolution but they also occupy and are adapted to different niches. So even if there is perhaps less than 1% percent divergence between the DNA sequence of humans and chimpanzees this relatively small difference amounts to a big difference at the level of behaviour. 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).

Although using homolog models has a natural appeal to most scientists, and it has indisputable advantages in scientific investigations, recent reviews suggest that human-ape comparisons also have clear limitations both from theoretical and practical points of view (Boesch 2007). The general problem with searching for the "key difference" between ape and human behaviour and cognition is that due to a lack of historical data there are problems in verifying the evolutionary scenario. In addition, the emphasis on a single "main" cognitive feature, as mentioned above (see: 1.1), obscures the real complexity of socio-cognitive behaviour.

As regards the validity and reliability of human-ape comparative results further concerns can be raised about 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. So the comparison becomes a difficult scientific endeavour because, behavioural 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 behaviour or the lack of species-specific experiences (see e.g. Bering 2004). For example, it has been argued that chimpanzees are tuned to view social interactions as being inherently competitive in nature (Hare & Tomasello 2005) in contrast to humans, and this would constrain their ability of using gaze direction as a behavioural marker for attention (Hare 2001). Therefore 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" captive apes are compared to a large number of children without accounting for the diversity of the apes or for their local ecological adaptations (see e.g. – Penn et al. 2008 versus Boesch in press).

Moreover, adult apes are often compared to human infants without controlling for external variables including previous experience and experimental/developmental factors. Ideally, 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 subjects 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 apehuman 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). A possible solution to this problem is the systematic modification of experimental variables so that the species assumed to be "inferior" could also be able to improve its level of performance ("positive control"). Unfortunately, however, human-ape comparative studies mostly fail to consider experience biases by the use of such positive controls.

Finally, the maintenance of apes and monkeys in captivity for experimental purposes creates an unsolvable welfare problem because these artificial environments cannot fulfil 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 increasingly accepted that it is high time to look for alternative and complementary paradigms. Such novel approaches may contribute a lot to exploring the evolutionary origins of the uniquely complex human cognition and behaviour.

1.3.2. Convergent modelling

Whilst 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, in order 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 behavioural (e.g., communication) modifications (see also Marino 2002).

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. 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 behaviour, 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 & Clayton 2001), but these are functionally restricted in the sense that they model only a narrow aspect of human behaviour.

Alternatively, the development of human-like behaviours 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 grey parrot provided evidence for conceptual quantitative ability (Pepperberg 1987), social learning and communicative abilities (Pepperberg & 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 behavioural 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.

It is also important to note, that when comparing analogies one should not assume similar mechanisms controlling the behaviour observed. For example, earlier several studies have reported that attachment behaviour in the dog-human relationship shares many features with the mother-child attachment in humans (e.g. Topál et al. 1998; Gácsi et al. 2001; Palmer & Custance 2008). Although the authors of these studies have argued for a case of analogy, nevertheless they do not claim that the very same behavioural mechanisms are at work or that the underlying neural organisation has the same complexity.

1.4 INTEGRATING HOMOLOGY AND CONVERGENCE: A TWO-DIMENSIONAL APPROACH FOR STUDYING SOCIAL COGNITION

The foregoing discussion on homology and analogy could lead one to argue for a different research concept, which actually integrates the two approaches. For such a strategy however, we need to broaden the number of species used to account for differences in the "homology" and "analogy" dimensions. Namely, such comparisons should include 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).

In addition to the species that are usually targeted in comparative cognition (apes, humans), the study of dogs and related canids may offer some interesting and novel avenues for research integrating homology and convergence. On the one hand, it is increasingly assumed that domestic dog (*Canis lupus familiaris*) is a promising candidate for convergent modelling as this species not only illustrates a single aspect of human behaviour but there is a complex level of similarity in a set of functionally shared behavioural features (see later for more details). Moreover dogs share many behavioural characteristics with their wild relatives and this offer the possibility of making interspecific comparisons within the framework of homologue modelling.

Following the suggestion of Timberlake (1993), aims of comparative research can be systematized in a two-dimensional space reflecting genetic relatedness and

ecological relevance (Table 1.4.1). Interestingly, the original suggestion concerned different combinations of species for each type of the four possible comparisons; however, in three out of four cases, members of the *Canis* genus offer valuable possibilities for comparative research.

Genetic relatedness					
		Low	High		
Ecological Relevance	High	Convergence dog versus human (e.g. communicative behaviour)	Microevolution wolf versus coyote (e.g. territorial behaviour)		
	Low	Classification dog versus human (e.g. manual abilities)	Homology wolf versus dog (e.g. territorial behaviour)		

Table 1.4.1 A general framework for comparing cognition and behaviour in the Canidae (based on Timberlake 1993). This table defines two independent dimensions (ecological relevance and genetic relatedness) which determine a "comparative matrix". Depending on the basic assumptions and questions research agendas may belong to different cells of this matrix (adopted for the specific case in *Canis*; from Miklósi 2007).

From the cognitive point of view, the idea of comparing behaviour and mental skills on the basis of homologies and convergences is important. The comparison of wolves and dogs is based on the assumption of a common ancestor living probably 25.000-50.000 years ago, and differences may reflect the specific changes in either the "lupus" or the "familiaris" route of evolution (e.g., Frank 1980; Kubinyi et al. 2007). That is, the wolf could provide a very important control for evaluating the behaviour evolution and in this sense the homologue relationship between dogs and wolves is equipotential to the relationship that exists between humans and apes. Accepting that the evolution of dogs has been affected by their long-term cohabitation with man, one may invoke concepts of convergence and ask whether the common environment has selected for commonalities in behaviour and mental skills in the case of dogs and humans especially with regard to sociocognitive abilities. Finally, interspecific comparison of wild-living canid species or subspecies may also be informative in terms of microevolution, looking at the evolutionary plasticity of the canis genome and how it may give rise to different local adaptations. Comparative research on wolves, coyotes, jackal species, or different types of feralized dogs, such as the dingo or New-Guinea singing dogs, has not been paid much attention so far. Undoubtedly, such work could also provide valuable insight for the evolution of cognitive skills in canids, and it would also place the more advanced wolf-dog comparisons into a better perspective.

Despite being aware of continuous changes in the evolution of the species, comparative cognitive (and behavioural) research is often based on a more static picture, mainly because we can work with only extant species. Thus, in contrast to morphological evolution, in which fossils represent species, there is much uncertainty about the timing of behavioural and mental changes. Moreover, there is the unvoiced assumption that some species included in comparative research have not changed over time. For example, extant chimpanzees may reflect a behavioural feature set that was typical for the common ancestor. Although this may or may not have been the case, there is little we can do about this in the case of Hominoidea. However, in the case of canids, the situation is somewhat different, because of the

more recent divergence of the species and the presence of a handful of relatively closely related extant forms (e.g., wolves, jackals, coyotes, dingoes) and their ecological variants. Thus, by looking at the phylogenetic relationships and even to present-day events, one can get at least some good estimation on the possible dynamics of the changes that may help to put our knowledge into a better perspective.

CHAPTER 2.

DOGS AS THE "NEW CHIMPANZEES" FOR COMPARATIVE SOCIAL COGNITION

2.1 THE EVOLUTIONARY ORIGIN OF THE DOG

The fascination with the somewhat bizarre association between humans and dogs has often diverted cool-headed attention from the evolutionary processes in the history of Canidae, and Canis in particular (but see Miklósi 2007; Wang & Tedford 2008). According to present knowledge, the story of the former began around 40 million years ago. These ancient canids and their relatives do not seem to be very specialized predators, and in many fossils we see trends toward an omnivorous diet. Nevertheless, the Canidae seem to be a very successful group of species, because, in contrast to their sister-taxa, they conquered the whole Northern Hemisphere including Eurasia and North America. The first species that are recognized as members of the Canis genus emerged in the Pliocene (5-6 million years ago), and they tended to be more specialized in hunting. Several Canis-species have controlled large herds of grazing mammals; some species gained in size and were regarded as top predators of the food chain. The last surviving member of these times was the large-sized Canis dirus, which lived until 10.000 years before the present in North America. In the last 100.000 years of their existence the dirus-wolf shared their habitat with populations of the Gray wolf (Canis lupus), which evolved in Eurasia but crossed to the New Continent. After the extinction of Canis dirus, the Gray wolf became the top predator throughout the Northern Hemisphere. This "status quo" changed only with the intrusion of humans that started at approximately 100.000 years ago, and the emergence of dogs is thought to have taken place sometime between 25.000-50.000 years ago in East Asia and/or the Near East (Hold et al. 2010: Savolainen et al. 2002).

This condensed history of the *Canis* genus revealed important lessons for the behavioural and mental evolution of these species. First, in contrast to other taxa of mammalian carnivores, canis-species showed a flexible feeding behaviour. This trait became especially advantageous in the case of dogs, and probably facilitated their association with humans who also show omnivorous tendencies. Second, in Canis we find a wide diversity of social systems, which may reflect some challenges of the selective environment. For the extant population of Gray wolves, it has been suggested that the dependency on large-sized prey may facilitate the existence of larger groups in which the individuals can cooperate in hunting (Mech & Boitani 2003). This flexibility in organizing social groups may have been a key factor in the success of the Gray wolf. Third, the last 100.000 years has witnessed a turn taking in glacial and interglacial periods. This meant that Gray wolves were faced relatively often with the need for accommodation to very different environmental conditions. One may hypothesize that this dynamic evolutionary scenario has "conditioned" the genetic material of the wolf for being able to support a very plastic phenotype with regard to behaviour and mental skills. It is easy to see how less specialised feeding habits, social flexibility, and genetic plasticity could have played a key role in the evolution of dogs in anthropogenic environments.

The social cognition of the domestic dog is the outcome of a many-thousand-years-long process during which the wolf-like capabilities were specifically transformed by the challenges of living with humans (Hare & Tomasello 2005). This account suggests that the evolutionary roots of the dogs' social cognitive skills cannot be understood by deeming the dog as a purpose-bred domesticated carnivore, only that it has been originally selected for hunting, herding, or guarding, and so forth. Instead, the transformation from wolf to dog can be viewed as a product of a more general process. In fact, recent findings provide some scientific support for the laypeople's belief that the dog is a peculiar species that was selected and formed by the man "in his own image." The notion that the transition from the wild state to the domesticated one had changed the selective forces radically, leading to the adaptive specialization of dogs in the human environment, has recently gained support from the dog-wolf and dog-human comparative studies on the social-communicative skills (see later for more details and Miklósi 2007 for a review).

2.2 THE CHANGING ROLE OF THE DOG IN THE HISTORY OF BEHAVIOUR SCIENCE

From the point of view of behaviour sciences dogs always had a doubtful status. They 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. latrans*; e.g. Fox 1971; Bekoff 1977; Frank 1980; Frank & Frank 1982.

The ethological description of the canidae was supplemented with the behaviour description of dogs (Fox 1971), and starting somewhat earlier dogs have been found to provide a good genetic model for investigation on social behaviour (Scott & Fuller 1965). Ethologists and comparative psychologists advanced a very different view on dogs, especially by recognizing the significant role of the evolved dog–human relationship (Hare et al. 2002; Cooper et al. 2003; Udell et al. 2009) but even in these studies the behaviour was described only as a kind of phenotype with little reference to the natural behaviour of dogs.

The situation changed toward the end of the 90ies when our research group initiated some studies on dog-human attachment and communication (Miklósi et al. 1998; Topál et al. 1997, 1998), which was followed by a series of investigations (for review see Miklósi 2007). The historical roots of this renewed interest can be found both in writings of Lorenz (1954) who emphasized the special relationship between man and his dogs, and in the work of Scott who used the dog as a model for understanding human attachment (Scott 1992). Although it is a trivial fact that the majority of dogs spend their life in or around human social setting, often in very close contact with humans (living in the family), it was only recently that this observation formed the starting point of ethological investigations on dogs.

Nowadays many agree that the natural place of the dog is around humans, so they can be just as rightful subjects of ethological studies if one observes them living in the human social group. This new approach soon proved to be very fruitful by leading to a large body of research in just few years and thus to the present-day renaissance of dog ethology.

In contrast to the dogs' fairly nice career as subjects of behaviour investigations, looking at the recent literature indicates that they are "newcomers" to comparative cognition research. This is really astonishing, because dogs have been around from the beginning of studies of animal minds. Among others, they were also the subjects of the famous experiments by Thorndike on problem-solving behaviour, and Lloyd Morgan (1903) who referred to the mental aspects of behaviour based on observation of dogs. However, except for a few isolated examples, research on cognition in dogs was nonexistent until the early 2000s. Edited volumes (e.g., Heyes & Huber 2000), and even more provocative accounts (Griffin 1992) on animal cognition contain very little, if any, reference to any member of the *Canis* genus, including man's best friend.

However, on the basis of recent experimental evidence (see Miklósi, 2007 for a review) it has been suggested that the dog presents a useful subject for the comparative study of human social evolution and this species may be the "new chimpanzee" for studies of comparative social cognition (Bloom 2004). The study of domestic 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. Nowadays, there is an increasing interest in comparative canid cognition and this newly emerging trend have led to intensive research programs on canine mentality, with ever-increasing numbers of papers published each year in the last decade.

2.3. THE CONTRIBUTION OF DOGS TO UNDERSTANDING SOCIAL COGNITION - WHY DOG IS AN OPTIMAL SOLUTION?

As indicated above, dogs could provide a valuable source for extending our understanding of the evolutionary processes that shape social cognition. Comparative work is an essential part of social cognition research and nowadays the dog seems to be definitely a rising star of this emerging line of research. Figure 2.3.1 clearly indicates that in the last few years something has changed about the dog in the field of cognitive science. This change stems from the recognition that domestic dog can offer novel aspects to the study of social cognition in an evolutionary framework.

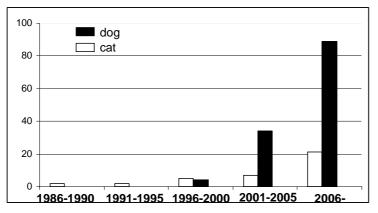


Figure 2.3.1.

The number of scientific papers published with the keywords 'social cognition' and 'dog' or 'cat'' in the last twenty five years (source: Scopus, 10.01.2011). The number of studies published on the social cognition of dogs increased significantly. The trend is even apparent in comparison with the number of papers aiming at

the social cognition of cats that are also domestic animals and, similarly to dogs, are commonly kept as pets.

(i) The first point of the dogs' privileged position in comparative cognition is the widely accepted notion that the dog is unique among domesticated species.

Generally speaking, 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). Importantly, although a handful of animal species have come into contact with humans through the process of domestication, the dog's origin dates back earlier than that of any other domestic species (Vilá et al. 1997; Savolainen 2002). Many argue that in the last 15-35.000 years dogs invaded the human niche, that is, the dog as a species has moved from the niche of its ancestor (which is shared by wolves) to the human niche. 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 hetero-specific social groups.

Evidently, the switch of niches by the dog could have been achieved only if it had been accompanied by some forms of behavioural change which enhanced their survival in human groups (e.g. Paxton 2000; Schleidt & Shalter, 2003). 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 (for an account of evolutionary processes that could have shaped behaviour of the dog, see Coppinger & Coppinger 2001). 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 1984) and more "novel" ones like assisting disabled people (James & MacDonald 2000). They provide also emotional support (Wells 2004) and participate in therapeutic programmes (Odendaal 2000).

As mentioned above (see: 1.4), domestication may have paved the way for some behavioural features in dogs that may converge to their human counterpart. As a result of cohabitation, dogs and humans share some particular social skills, thus dog domestication provides a typical case for convergent evolution. Evolutionary parallels can also be observed in cats or horses, where the domestication process has contributed to their adaptation to the human environment, however, in these non-canine 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 & Cook 1996; Bradshaw et al. 1999).

(ii) The second, point of the dogs' "rising star" status in comparative cognition lies in the fact that human social environment seems to provide a natural niche for dogs.

Compared with monkeys and apes studied mainly in captivity and under semi-natural conditions, dogs, like human children, can be observed in their natural environment. Dogs are prepared in an evolutionary sense to live in the human environment, while apes, monkeys and other species need to be individually socialized to be available to such comparative research. 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 (Riedel et al. 2008; and see also our experimental data later). 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 inter-specific contact can be re-established rapidly because the genetic variability between pet dogs and stray or feral dogs is smaller than the environmental variability causing behavioural

differences in these phenotypes (Boitani et al. 1995). Since pet dogs can revert to feral life within a few generations (Daniels & 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 behaviour towards humans in the case of both dogs (Scott & Fuller 1965) and humans (Candland 1993).

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. A somewhat more detailed discussion of the term *enculturation* and the significance of this phenomenon in studying dogs' social cognitive skills will be given in the next section (2.4.).

All in all it follows that dogs can and should be studied in their natural group, that is, where and when they are living with humans and we should combine the methods of naturalistic observation and experimentation on hetero-specific groups involving dogs and their owners. This approach provides a very useful way of studying dog social cognition and may also be useful 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.

(iii) Third, the dog has a living ancestor, the wolf.

Comparison with the ancestor is important for convergent modelling and dogs offer a unique opportunity for making behavioural comparisons not only with the "niche-mate", the human, but also with the living ancestor, the wolf (Canis lupus). 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 (see e.g. Kubinyi et al. 2007). For example, wolves show complex social behaviour involving cooperation in hunting and parental care, expressive means of communication and context-dependent dominance relationships (Mech & 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 behaviours. 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).

(iv) Fourth, it is also an important point, that 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 behaviour 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, and at the same time, (at least partly) eliminates reliability and welfare concerns relating to research on apes and monkeys (see also above: 1.3).

It is also important that 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). Thus 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. 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.

For example, some early observations showed that dogs living in the garden are more persevering and independent in new problem-solving situations than dogs sharing the flats of their owners (Topál et al. 1997). Others have reported that dogs from more rural areas are also more territorial, less fearful, and have less social contact with their human owners in comparison to urban companions (Baranyiova et al. 2005). Questionnaires may also provide a useful tool to inquire about "cultural effects", such as attitude to dogs, views on the dog-human relationship, as well as about intersubjective ways of investing in the relationship, including training and spending time together. A recent large-scale study involving over 14.000 people showed that quite a few aspects of the ownership may influence the behavioural traits (personality) in pet dogs (Kubinyi et al. 2009). For example, sociability, which may be an important factor in experimental investigations, was influenced by the training experience and interaction with the owner.

(v) Finally, the dog is a promising candidate species which have the potential to become a non-invasive model of neuroscience.

It is increasingly assumed that dogs can be a model for an alternative neurobiological approach favouring modern non-invasive techniques of neuroscience. In general, all methods that are presently available and ethically applicable to humans can be utilized in freely living populations of dogs. Several methods like these are available which if applied it simultaneously, could have a powerful effect. A starting neurogenetic approach could be based on the effects of allele polymorphisms on behaviour. For example, in the case of the dopamine DRD4 receptor an association with temperament-related behavioural traits has been described in humans (Lakatos et al. 2000). Recent molecular genetic investigations revealed the presence of an analogue polymorphism in dog DRD4 receptor (Ito et al. 2004). The implication of this polymorphism in human attachment (Lakatos et al. 2000) has potential for the elaboration of a dog model. Sequencing of the dog genome has put mechanistic approaches of behavioural and mental skills into a novel perspective. Moreover it is to be expected that the genome sequence of other canids will also be available shortly, which offers an unprecedented possibility to gain some insight into the changes of the genetic causes of behavioural and mental differences.

However, such genetic data can be utilized only if the phenotype is characterized under well-described conditions (Miklósi 2007) and comparable comparative investigations are available. The non-invasive measurement of physiological parameters like heart rate variability or hormone levels (cortisol, testosterone) could also reveal psychophysiological changes paralleling sociocognitive behaviour (Maros et al. 2008).

It has often been observed that in certain situations dogs express abnormal behaviours which show a close correspondence to human neuropsychiatric conditions. In line with this recent studies have advocated the use of dogs as natural models of human psychiatric conditions (Overall 2000) and dogs proved to be also a useful model species for tracing mental changes in human ageing (Tapp et al. 2003; 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 behaviour or the extension of life expectancy in some dog populations due to increased protection from environmental challenges.

2.4. ENCULTURATION: WHAT DOES THIS MEAN FOR COMPARATIVE COGNITION OF CANIS?

2.4.1. Enculturation as the desideratum for dog development

If we accept the theory of domestication for dogs (see above), then, by "default", the dogs' natural environment is the human family or some form of social grouping. This means that dogs have been selected for being enculturated, that is, their natural development depends on specific physical and social input from the human environment. It follows that, albeit dogs survive also outside the anthropogenic environment, this should be regarded as a deviation from the natural route of development. Not everyone agrees with this view, and many regard feral dogs as the true representatives of the species and think about socialized dogs as a special scenario of the individual development.

Importantly, in the case of enculturated apes, the situation is reversed because they have not been specifically selected for sharing the human social environment. The relatively straightforward enculturation of apes is rooted in our common evolutionary heritage. Experimental observations suggested that apes raised in intensive human contact performed superiorly in comparison to less well socialized conspecifics. These led researchers to assume that enculturation may change the mental (psychological) stance of these animals making them more "human-like" (Tomasello & Call 1997, but see Tomasello & Call 2004). These observations generated a debate about whether enculturation causes mental changes that surpass the natural boundaries of species-specific cognitive skills or whether such experience increases the familiarity of the testing environment and facilitates learning in general (Bering 2004; Suddendorf & Whiten 2001).

Without taking sides, it is clear that, for apes, enculturation is not a part of the natural developmental scenario, and it may be that, despite all types of social-environmental enrichment in captivity, wild chimpanzees possess even more sophisticated social skills (see also Boesch 2007 for review). Thus, enculturation may also influence socio-cognitive skills in dogs but, in contrast to the chimpanzees, this may reflect the natural situation. It follows that, if some form of enculturation is

requisite for normal social development of the dog, then all other cases should be seen as representing some form of social deprivation. This is important because social skills are often portrayed as being the outcome of a complex epigenetic process. Thus, comparing the situation in apes and dogs, we propose that enculturation of the former is a kind of social enrichment or "luxury," whereas in dogs it is a precondition. Apes missing intensive social contact of humans should be considered as normally developing animals; however, non-enculturated dogs are socially deprived.

2.4.2. Enculturation as a procedural factor

In addition to the aforementioned differential functional effect of socialization on apes and dogs, the issue of enculturation inherently raises methodological problems of experimental design. Most experiments rely heavily on anthropocentric procedures; thus, only well socialized animals are expected to participate with any chance of success. Eventually, this has lead to the intensive socialization of apes, but, in parallel, no such extra effort is needed in the case of family dogs. Some form of socialization or enculturation is generally used in the process of upbringing experimental animals, although it may vary depending on the species and laboratory practice. It is, however, problematic that such interventions are rarely quantified making comparisons both within and among species very difficult.

Paradoxically, researchers often assume that enculturation has a strong effect on the behaviour of the prospective experimental subjects, but there is little tendency to explain the nature of these effects. Variations in the enculturation procedure might include the timing of the early socialization period, the degree of social experience (e.g., number of familiar persons, type of interaction), and some specific training and execution of social routines. Sparse data in the literature on socialization in wolves shows that the time and extent of separation from conspecifics (preferably as early as 4–6 days after birth), the experience of humans, and the nature of social interaction influences the behaviour of enculturated wolves. Differences in temperament may have also contributed to the difference in responsiveness to enculturation (Hare & Tomasello 2005). Selection for tameness, which can manifest as a reduced fear from non-conspecifics (decreased neophobia) resulting in less fear-related aggression, could contribute to better interspecific social skills and social interactions with humans.

Recent observations show that the performance of wolves in food-finding tasks in which they have to rely on human gestures depends on how these animals have been socialized (Hare et al. 2002; Miklósi et al. 2003; Udell et al. 2008). Wolves that were socialized in a more intensive way and may have been exposed to specific forms of training may perform better in such tasks compared to conspecifics with less experience. Although this may sound trivial, the lack of exact information about the enculturation process hinders the interpretation of these effects in all species of Canids.

Given the assumption that the species differ in their genetic constitution, only a qualitatively and quantitatively equivalent enculturation procedure can allow us to connect the observed behavioural or cognitive differences to evolutionary scenarios. This simple insight provided the basis for a recent comparative research program on wolves and dogs (Kubinyi et al. 2007) during which members of both species were enculturated in a similar manner. The 24-hour-long togetherness with the wolf cubs

for the first four months, exposure to many different types of humans providing variable social experience, and little direct training (apart from some experimental test situations) have been thought to be the minimal social experience for successful experimental work with wolves. Importantly, this amount of enculturation is already more intensive than everyday dogs would experience; therefore, for comparative observations, dogs were raised in the same way (for more details and experimental results see below in Part II.).

It is also important to note that the cessation of enculturation may affect enculturated wolves and dogs differently. Anecdotal observations suggest that wolves may become deculturated more rapidly than dogs. However, the deculturation process in dogs should not be equated with deprivation, that is, lack of stimulus input during development. Dogs living in the shelter, depending on their (often uncertain) history, may or may not have been subjects of either a deculturation or a deprivation process. Shelter dogs follow a different developmental route with regard to human social experience. Thus, the socio-cognitive behaviour and performance of such populations may be affected by several complicating factors. This should prohibit the utilization of these animals for providing evidence for the lack or the need of enculturation on the normal development of socio-cognitive skills in dogs (Hare et al. 2010; Udell et al. 2008).

Finally, there are two important aspects of the enculturation process that are often not articulated. First, the individual shows differential sensitivity for social input during development. The behavioural and cognitive skills unfold in a predetermined sequence that determines to some degree what kind of environmental and social input is needed or expected. Second, environmental input may irreversibly change, to some extent, the course of events in a developing individual, and the enculturation process can be conceptualized as acting through positive feedback loops: the more social experience is gained the larger the capacity emerges for more social experience. This also means that social input early in development plays a more significant role than later influences, and actually later social effect may depend critically on the earlier social experience.

2.5. OPERATIONAL FRAMEWORK AND WORKING HYPOTHESIS

Human-dog comparisons have already been initiated long ago (e.g., Scott & Fuller 1965; Scott 1992), especially with regard to social behaviour. 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 & Shalter 2003), and analogies have been argued for in the case of social-communicative skills (Hare & Tomasello 2005) and personality models (Jones & Gosling 2005). Either explicitly or implicitly, recent enthusiasm for studying dogs reinforces the view that this animal species can provide a unique possibility for modelling human behaviour.

As mentioned earlier (see 1.1), in explaining human evolution at the behaviour level Csányi (2000) has proposed a number of changes that took place in parallel and led to the emergence of Homo sapiens in contrast to a single factor models, which emphasise the primacy of one major trait (e.g. tool making).

In line with the aforementioned strong version of the domestication hypothesis suggesting that caninization and hominization can be seen as convergent evolutions during which functionally human-analogue behaviours emerged in dogs (see 2.3), we can propose a similar approach in the case of the dog, where it is likely that many relatively small but definite changes lead to a behaviourally very different species in comparison to the wolf ancestor. 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 behaviours. That is this approach aims at finding out whether and how the interaction between separate behavioural changes leads to the accumulation of social skills that could resemble in many respects the human social behavioural system.

Accordingly we may assume that the comparative study of social cognition in dogs has the potential to answer questions regarding the functionality of human behavioural components and the following working hypothesis could provide an operational framework for this.

Main components of the working hypothesis:

- (i) The three main dimensions of the human behaviour complex (sociality, behavioural synchronization and constructive skills see 1.1.) are assumed to have undergone changes after the *Pan-Homo* split.
- (ii) Taking a behavioural 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.
- (iii) 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), the evolution of dogs may mirror some aspects of hominization.
- (iv) It follows from this that many social skills in dogs have undergone convergent evolutionary changes and the study of the behavioural convergences between dogs and humans offers a comprehensive framework for understanding the evolutionary emergence of human social behaviour (see also section 2.3).
- (v) The model developed for the description of human behaviour traits (i.e. human behaviour complex, see 1.1.) might provide a useful framework with which to conceptualize evolutionary changes in dogs. The "dog behaviour complex" defines those components of dog behaviour 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 behaviour complex because of evolutionary constraints including differences in anatomy and cognitive processing (e.g., lack of linguistic skills in dogs, differences between dogs and humans in their ability to manipulate objects etc.). However, the overlapping elements of human- and dog behaviour complexes help to identify the minimum set of skills that had to be present at the beginning of Homo evolution. Thus the study of "dog behaviour complex" can capture some aspects of the early stage of hominid evolution when people evolved a set of social skills that provided the basis for complex interaction and it can also show that complex social behaviour and interaction at the group level is possible even in the absence of linguistic abilities.

PART II.

IN SEARCH FOR THE FUNCTIONAL ANALOGUES OF HUMAN SOCIAL COGNITION IN DOGS – EXPERIMENTAL STUDIES

Recent research has just begun to show that wolf-dog-human (infant) comparative triangulation could shed light on the infant-like functional aspects of dogs' social cognition (see Miklósi 2007 for a review) and in the second part of the thesis we will show empirical findings with respect to those components of the "dog behaviour complex" (i.e., interpsecific social attraction and attachment; social skills for behavioural synchronization; behavioural manifestations of the constructive character of communication skills) that can facilitate the manifestation of complex interactions at the group level. However, we have to keep in mind that convergent behaviour modelling emphasizes the surface similarity of the behaviour, 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. Consequently, heated debates about the hidden mental factors and underlying mechanisms (see e.g., Reid 2009; Udell et al. 2009) may turn out to be unproductive; they divert our attention from the more pragmatic, functional aspects of behaviour, especially if the underlying evolutionary factors are still not clear. From the functional viewpoint, no matter if dog-wolf differences and dog-human similarities lie in specific (qualitative) changes in the dogs' cognitive processing or far less specific (quantitative) changes in the attention and memory skills and associative learning capacities etc.; in reviewing parallels between human and dog behaviour, it is better to refrain from premature interpretation of the cognitive processes that control the observed performance.

CHAPTER 3.

SOCIALITY

There are three main factors in the "sociality" domain of Dog Behaviour Complex which influence dog-human social relationships: social attraction, attachment and agonistic behaviours.

The behavioural 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 non-human 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 towards 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 towards humans after only a brief exposure (Stanley & Elliot 1962) and despite being punished for social contact (Fisher 1955). In fact, anyone who has raised wolves and developed a close relationship with them has noticed major differences between human-oriented social behaviour in dogs and wolves (e.g., Fox 1971) .Comparative experiments provided various types of evidence that overall dogs show a stronger attraction toward humans than wolves show toward humans (Zimen 1987; Frank & Frank 1982).

As regards the agonistic aspects of social behaviour, wolves are often portrayed as being fiercely aggressive animals, in contrast to the gentle manner of "man's best friend". Both classic studies (Scott & Fuller 1965) and recent accounts (Hare et al. 2005) have assumed that selection has led to reduced aggressive behaviour 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 behaviour more frequently than wolves of similar age (Feddersen-Pettersen 1986).

In the following two studies (STUDY I & STUDY II) we aimed to investigate the early social behaviour of hand-reared dogs and wolves in a comparative manner. We have hypothesized that if the environment of wolves and dogs is equalized then the remaining behavioural differences could be explained in terms of inherited factors (and/or maternal prenatal influences).

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3.1. STUDY I. SOCIAL BEHAVIOUR AND SOCIAL ATTRACTION TO HUMANS: COMPARISON OF EXTENSIVELY HAND-REARED DOG PUPPIES AND WOLF PUPS.*

Abstract

It has been often argued that the sophisticated social behaviour of dogs is mainly the result of environmental influences dominated by human intervention. In this regard one crucial point is, whether there are species-specific behavioural or cognitive differences after a similar manner of enculturation of dogs and wolves if the amount of socialization remains within the normal range that is typical for dogs living in social environments. In order to reveal early species-specific differences, we observed the behaviour of dog puppies and wolf pups hand raised and intensively socialized in an identical way. The pups were studied in two object-preference tests at age 3, 4, and 5 weeks. After a short isolation, we observed the subjects' behaviour in the presence of a pair of objects, one was always the subject's human foster parent (caregiver) and the other was varied (nursing bottle, unfamiliar adult dog, unfamiliar experimenter or familiar conspecific age mate). Although dogs and wolves did not differ in their general activity level during the tests, they showed species-specific differences in the social preference towards their human caregiver. Moreover, wolf pups were more likely to show aggressive behaviour toward a familiar experimenter and also seemed to be more prone to avoidance. In addition to these differences, compared to wolves, dogs tended to display more communicative signals that could potentially facilitate social interactions with humans.

These results demonstrate that already at this early age—despite unprecedented intensity of socialization and the comparable social (human) environment during early development—there are specific behavioural differences between wolves and dogs mostly with regard to their interactions with humans.

Gácsi M, Győri B, Miklósi Á, Virányi Zs, Kubinyi E, Topál J, Csányi V (2005). Species-specific differences and similarities in the behaviour of hand raised dog and wolf puppies in social situations with humans. Developmental Psychobiology 47(2): 111-222.

^{*}Based on:

INTRODUCTION

Although dogs and wolves seem to be similar in their social developmental processes with regard to conspecifics, some marked differences in their behaviour toward humans have been observed (Frank & Frank 1982; 1985). However, previously there have been rather few research programs using wolves and dogs with similar rearing history (Frank & Frank 1987) but even in these studies, the sample size was small so it was difficult to clearly establish the genetically based behavioural differences. Feddersen-Petersen (1986) compared the intraspecific behaviour of young wolves and dogs having limited contact with humans. Others have raised wolves and dogs in human environments (Fentress 1967; Frank 1980; Frank & Frank 1982; Frank et al. 1989; Woolpy & Ginsburg 1967) in order to investigate motivational and cognitive differences. Such comparative research usually assumes that the revealed species characteristics and/or specific differences reflect the influences of differential genetic determination. With the same general assumption, our research program is distinctive in two very important aspects from earlier ones.

First, we decided that both dogs and wolves should experience the same and especially intensive socialization by humans. That is, each human caretaker spent the first 2–4 months with one individual by providing care for 24 hr a day. Observations that humans can only socialize wolf pups successfully if they are separated very early (before eye opening) from the mother (Klinghammer & Goodmann 1987) suggest very early learning and/or strong genetic preference of conspecifics in the wolf. So we planned our socialization regime especially carefully to exclude results deriving only from the differing sensitivity for early socialization in the two species.

Second, we socialized a relatively great number of individuals in order to have more chance to discriminate behavioural traits that are exclusively specific to one of the species (qualitative differences) from those that are present in both species and possibly represent two extremes of the same distribution (quantitative differences).

In the first experiment, we wanted to see whether members of both species developed similar preference for their primary (human) caregiver. For the testing, we have applied an object-preference test, a method often used to look for early effects of social experience. The subject usually has the opportunity to choose between two (social or nonsocial) simultaneously presented objects by spending more time with one or the other stimulus object (e.g., Sackett et al. 1964). This method allowed us to use a natural set-up that interfered relatively little with the behaviour of the subjects. Because of earlier indication for differences in temperament traits already at this age (e.g., Frank & Frank 1987), we have also measured signs of aggressive and avoidance behaviour.

In previous studies, we have provided evidence that dogs have an advantage to use face and eye-related gestural cues (e.g., Soproni et al. 2001). Further, there appears to be a species-specific difference in the use of face/eye contact in social interactions with humans when comparing 4-month-old wolves and dogs (Miklósi et al. 2003). To address this question, we investigated whether the species-specific differences can be traced back to an earlier stage of development, and in a second experiment (Reinforced Eye Contact tests) we tried to study whether these differences can be masked by learning procedure.

METHODS

Subjects

In year 2000–2003, our group raised 13 gray wolf pups (*Canis lupus*) born at Horatius Ltd. Animal Park (6 males and 7 females, from five different litters) and 11 dog puppies (*Canis familiaris*) from three shelters (6 males and 5 females from five different litters, all mongrels). All the animals were socialized and tested the same way. Not all of the subjects could participate in every test and in some cases (9 subjects' 16 tests from the total 144 tests), the data were lost due to technical problems.

Socialization Procedure

Subjects (dogs and wolves) were individually hand raised by humans after being separated from their mothers and littermates on Day 4–6 after birth (before their eyes opened). Each subject spent the first months of their lives in 24-hr close contact with their human foster parents, they lived in the homes of the caregivers and slept together with them at night. They were bottle-fed and from the age of 4–5 weeks hand fed also with solid food. The caregivers carried them in a pouch, so the pups could participate in their everyday activities (travelling by public transport, attending classes at the university, visiting a friends, etc.). The pups frequently met unfamiliar humans, and at least twice a week they also met conspecifics of about the same age and adult dogs. This way, they were regularly exposed to novel stimuli and situations as well as to familiar individuals.

At the age of 4 months, wolves were placed back at the animal park where they could interact daily with humans and other wolves whilst dog puppies were adopted by their caregivers (N = 7) or by others (N = 4).

Our team was licensed by the Department of Nature Conservation, Ministry of Environmental Affairs (No.3293/2001) to hand rear and expose the wolf pups to extensive socialization, and our department has also been licensed by the Ethical Committee for Animal Experimentation at the Eötvös University to conduct such research.

3.1.1. EXPERIMENT I/1

Experimental procedures - Object-Preference Test

The subjects were presented with all together six object-preference tests; two tests were conducted on every subject at the age of 3, 4, and 5 weeks. On each occasion, all subjects were observed first in the first test one-by-one and then in the same order in the second test. The tests were performed in the morning and the caregivers fed the animals with milk at least 2 hr earlier. Before the tests, each subject was isolated for 5 min in a 9 m x 9 m x 9 m cardboard box situated in an unfamiliar empty room. (This was done in order to elicit similar motivational levels in all pups to initiate social interactions during the test.) The subjects was put into the box and taken out of it by a familiar female experimenter.

Following the isolation period, the subject was carried into another room (2.6 m x 3.6 m) that was unfamiliar to them at the first occasion (at the age of 3 weeks).

The subjects' behaviour was observed for 5 min (see Figure 3.1.1.1. for the testing design).

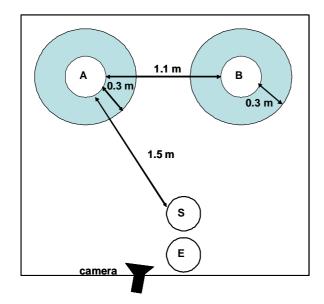


Figure 3.1.1.1. Schematic illustration of the test room. (A) and (B) indicate the position of the two different types of objects that were presented simultaneously during the 5-min tests (caregiver, experimenter, adult dog, conspecific pup, milk bottle according to the type of the test). The objects' location (right or left side) counterbalanced on the same day. The grey-shaded areas represent the proximity of the objects. At the beginning of the object-preference test. familiar female experimenter

(E) put the subject (S) on the starting point, which had been marked on the floor. The two objects were 1.1 m from each other and 1.5 m from the subject's starting position. A cameraman, standing behind a 1.2 m high plastic screen, recorded the tests with a camera positioned on a tripod.

Object Pairings

In all tests, the caregiver of the subject was one of the objects ("reference") who were paired with different kinds of other social objects with the only exception of the nursing bottle in the very first test (see Table 3.1.1.1). The human participants always sat cross-legged and motionless on the floor quietly facing the subject. Their hands were placed on the floor in front of them with upturned palms.

3 Weeks (20–22 Days)	4 Weeks (27–29 Days)	5 Weeks (34–36 Days)				
5-min isolation in box						
Bottle-caregiver object-	Conspecific pup-caregiver	Dog-caregiver object-				
preference test	object-preference test	preference test				
$(N_{(W)} = 12, N_{(D)} = 9$	$(N_{(W)} = 9, N_{(D)} = 8)$	$(N_{(W)} = 12, N_{(D)} = 11)$				
10–15-min in pen						
5-min isolation in box						
Dog-caregiver object-	Experimenter-caregiver	Experimenter-caregiver				
preference test	object preference test	object-preference test				
$(N_{(W)} = 12, N_{(D)} = 11)$	$(N_{(W)} = 12, N_{(D)} = 11)$	$(N_{(W)} = 12, N_{(D)} = 11)$				

Table 3.1.1.1. The sequence of testing at the age of 3, 4, and 5 weeks

Note. On each occasion, the procedure started with a 5-min-long isolation. Immediately after the isolation, subjects participated in the first object-preference test. It was followed by a 10–15-min period when the animals rested in the pen. Then the pups were isolated again and the second object-preference test came next. The number of participating subjects is indicated in case of each test (some of the tests could not be analyzed due to technical problems; these are omitted from the table).

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Bottle-Caregiver

There was some lukewarm milk (used for feeding) in the nursing bottle that was placed on a small cloth soaked with milk. The caregiver was looking at the subject during the test.

Experimenter-Caregiver

Both humans were looking at the subject during the test. In both tests, the same female experimenter took part. At the first time, she was unfamiliar to the subjects, and did not have any contact with them between the similar tests at the age of 4 and 5 weeks.

Dog-Caregiver

The adult dog was positioned facing the starting point of the subject. He was a well-trained, adult Belgian shepherd male that at the time of the first test was unfamiliar to the subjects and had no contact with them apart from the tests. The dog lay calmly at his place for 5 min. This time the caregiver adjusted her behaviour to that of the adult dog, that is, she oriented to the subject only when the dog did so.

Conspecific Pup-Caregiver

We always selected a same age sleeping conspecific from the subject pool in order to avoid interactions. Conspecific subjects knew each other equally well, as they had the possibility to meet regularly from the age of 2 weeks. The sleeping pup was gently placed to the floor and watched for a few seconds whether it was lying calmly. The caregiver sat motionless looking at the subject.

Data collection and analysis

As the duration of the test sessions varied slightly, we calculated the relative percentage of the time spent with each behaviour.

Activity (%)

In this early age, social behaviour obviously cannot be analyzed without considering the animals' general mobility or activity level. Taking into account the immature motor behaviour of the subjects, we assessed activity observing the time (s) spent standing or moving on four legs. (We only considered the time when the subjects were not in physical contact with the objects.) For statistical analysis, we used the mean activity value measured in the two tests on the same day. Activity level at the age of 3 weeks = $(A_1/t_1 + A_2/t_2)/2$.

 $(A_1 = \text{time standing or moving on four legs during the first test at the age of 3 weeks, t_1 = \text{total time of the first test at the age of 3 weeks, A_2 = \text{time standing or moving on four legs during the second test at the age of 3 weeks, t_2 = \text{total time of the second test at the age of 3 weeks.)}$

Proximity (%)

We measured the relative duration of the total time spent in proximity with each object closer than the length of the subject's own body (i.e., the subject is closer than approximately 25–35 cm to any part of the stimulus). For statistical analysis, a preference index was calculated (see below).

Vocalization (%)

The relative duration of the total time spent with any form of vocalization. For statistical analysis, we used the mean vocalization value measured in the two tests on the same day (same calculation as in case of activity). The occurrence of vocalization (score, 0–1) was also recorded by the familiar experimenter just before she entered the room where the subject was isolated.

Gazing at Face (Relative Frequency)

Gazing was defined as orienting the nose toward the human's face, which was characterized by lifting of the head. This variable was recorded only while the animal was in proximity with a human (caregiver and unfamiliar experimenter). The frequency of gazing at human face was calculated by dividing the number of gazings by the time spent in proximity with the humans. For statistical analysis, we used the mean of gazing frequencies measured in the two tests on the same day. (The adult dog's eyes were not high enough to identify the subjects' head movements as gazing.)

Tail Wagging (Score, 0–1)

The subject was given a score 1 if it wagged its tail when approaching either of the objects for the first time (getting closer than 30 cm) or while first getting into physical contact with either of them. A score 0 was given if this behaviour was not observed on these occasions or the animal did not get into proximity with a stimulus during the test.

We have recorded signs of avoidance and aggressiveness of the subjects toward the approaching familiar experimenter both before and after each test when the animal was handled: first, at the end of the isolation periods when the familiar experimenter took the subject out of the box and for the second time, when she slowly approached, caught, and lifted the subject at the end of the object-preference test.

Avoidance (Score)

The subject scored 1, if it showed avoidance toward the familiar experimenter, or a score 0, if it did not show avoidance (i.e., behaved passively or approached her).

Aggressiveness (Score)

We categorized the reaction of the animal as aggressive if it growled or tried to bite the familiar experimenter. The subject was given a score 0 if it showed no aggression toward the familiar experimenter and a score 1, if it growled or tried to bite.

All object-preference tests were videotaped and analyzed later. Interobserver agreement between her and a naive observer on the behaviour categories was assessed by comparing their parallel coding of the same video records and evaluation of the 22% of the data (eight wolves, eight dogs). The following Cohen Kappa results were obtained (Martin & Bateson, 1986): activity = 0.85; proximity = 0.96; vocalization = 0.76; tail wagging = 1; gazing at face = 0.93; avoidance = 1; aggressiveness = 1.

In the case of proximity, we have calculated a preference index as follows: (relative duration of time spent with caregiver-relative duration of time spent with

other object)/(relative duration of time spent with caregiver + relative duration of time spent with other object). In case of the preference index, first we tested for divergence from zero (i.e. no preference) by one-sample t-tests. Then we compared the preference index of dogs and wolves by one-and two-way ANOVA. We scored it as missing value, if the denominator was zero (no time spent in proximity of any of the two objects). 'Gazing at face' did not show normal distribution, therefore nonparametric Mann–Whitney U-test was used for analysis. 'Tail-wagging', 'avoidance,' and 'aggressiveness' were analyzed with Fisher exact test.

RESULTS

Activity

First of all, we wanted to determine whether there was any difference in the motor ability or general activity level of the species during the object preference This was measured by calculating the mean activity level for the two tests at all three ages. The two-way ANOVA (species x age, with repeated measures for age) revealed no difference between the activity level of the wolf and dog pups at any age (F(1,20) = 1.878, p = 0.186). However, the subjects spent more time with active behaviour as they got older (F(2,40) = 7.995; p = 0.001) (Figure 3.1.1.2). The species-age interaction was not significant (F(2,40) = 1.649; p = 0.205).

Proximity (Preference Index)

To assess the social behaviour after a short isolation, we compared the time spent in close proximity to the objects presented. Comparing the preference index to zero (assuming no preference for either object presented), we found that both dogs and wolves tended to show either no preference at all or preference for the caregiver. Wolves preferred to be in the proximity of the caregiver in two tests: at the age of 3 weeks (Bottle-Caregiver) and at the age of 5 (Experimenter-Caregiver). Dogs tended to spend more time with the caregiver in three tests: at the age of 4 weeks in both tests (Pup-Caregiver and Experimenter-Caregiver) and at the age of 5 (dog-caregiver) (see Table 3.1.1.2).

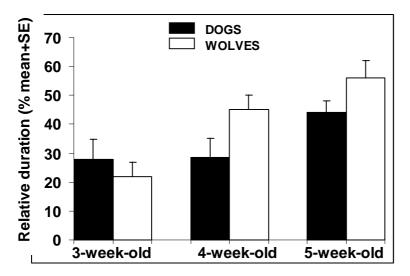


Figure 3.1.1.2. Mean value (+SE) of relative durations of the time spent in activity at the age of 3, 4, and 5 weeks averaged the results of the two object-preference tests. The comparison of the activity values at different age categories repeated-measures **ANOVA** revealed significant difference between wolves and dogs. The activity increased with age, the species-age interaction was significant.

	3 Weeks	4 Weeks	5 Weeks
	Bottle-caregiver	Conspecific pup-caregiver	Dog-caregiver
Wolves	t(9) = 5.489,	t(8) = 1.043,	t(11) = -0.524,
	p < 0.05	p = 0.327, ns	p = 0.611, ns
Dogs	t(4) = 0.662,	t(5) = 3.83,	t(9) = 12.131,
	p = 0.544, ns	p < 0.05	p < 0.01
			Experimenter-
	Dog-caregiver	Experimenter-caregiver	caregiver
Wolves	t(10) = 1.664,	t(9) = 1.648,	t(11) = 3.768,
	p = 0.127, ns	p = 0.128, ns	p < 0.01
Dogs	t(7) = 0.777,	t(9) = 2.72,	t(9) = 1.532,
	p = 0.462, ns	p < 0.05	p = 0.159, ns

Table 3.1.1.2. Results of the Comparison of Preference Indexes in all Tests Note. The differences of the preference index from zero were analyzed with one-sample t-tests, and the p-values were corrected with False Discovery Rate adjustment (Benjamini et al. 2001). In all cases, significant differences (highlighted with bold face) refer to preference to be in the proximity of the caregiver.

The preference index of dogs and wolves was compared by one-way ANOVA in case of the two pairings that were carried out only once (Bottle-Caregiver and conspecific Pup-Caregiver). Two-way ANOVA (with repeated measures for age) was used to compare the species in those two pairings (Experimenter-Caregiver and Dog-Caregiver), which were tested two times (at different ages).

We found no difference in the preference index of dogs and wolves at the age of 3 weeks in the Bottle-Caregiver test (F(1,14) = 2.54, p = 0.135) and also at 4 weeks of age in the Conspecific Pup-Caregiver test (F(1,14) = 0.77, p = .395).

Similarly, no effect of the species has been found in the Experimenter-Caregiver tests (F(1,17) = 0.05; p = 0.824), lacking also the effect of age (F(1,17) = 0.113; p = 0.74) and interaction (F(1,17) = 0.45; p = 0.24). The Dog-Caregiver tests also showed no overall difference in the social preferences of the two species (F(1,16) = 2.16; p = 0.16) and no effect of age was found either (F(1,16) = 0.04; p = 0.84). However, the significant interaction (F(1,16) = 7.08; p = 0.02) indicates that compared to wolves dogs showed more pronounced preference for the caregiver when they were 5 weeks old.

It also seemed informative to analyse which unfamiliar social partner (experimenter or dog) took greater effect on the animals in the presence of the caregiver, that is, in case of which object they showed less preference toward the caregiver. Comparing the preference index values in the two tests at the age of 5 weeks, we found that dog puppies tended to prefer the caregiver less if the other object was the unfamiliar human (t(8) = 2.77, p = 0.024) while wolf pups showed less (actually no) preference toward the caregiver when the other choice was the unfamiliar adult dog (t(11) = -3.84, p = 0.003) (Figure 3.1.1.3).

Vocalization

During the isolation period, distress vocalization was characteristic mainly for dogs. While seven of eight dogs vocalized (high pitched sounds or howl) at least on one occasion just before the experimenter entered the room, only three of nine wolves showed similar behaviour. All vocalizations were high-pitched sounds (e.g.,

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whining or yelping: see Cohen & Fox 1976; Ohl 1996) thus reflecting most probably signs of distress because the animals vocalized mainly when they were not in the proximity of the objects. Using two-way ANOVA (with repeated measures for age), we have found that dog puppies spent more time with vocalization during the tests than wolf pups did (F(1,20) = 1.24; p = 0.003) without an effect of age (F(2,40) = 1.954; p = 0.115). However, significant interaction (F(2,40) = 3.912; p = 0.028) indicated that the tendency for vocalization decreased with age in dog puppies, while in case of wolf pups, no such change was evident (Figure 3.1.1.4).

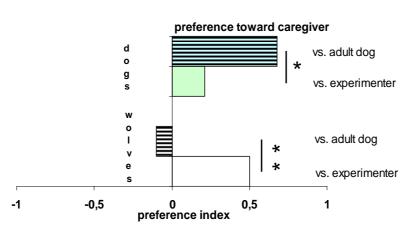


Figure 3.1.1.3.

Preference index values of 5-week-old dogs (two upper bars) and wolves (two lower bars) in the "Caregiver-Dog'' (filled bars) and the "Caregiver-Experimenter' (dotted bars) object-preference Index tests. values different from zero refer to preference to be in the proximity of the indicated objects. The

index values were calculated as: (relative duration of time spent with caregiver – relative duration of time spent with other stimulus)/(relative duration of time spent with caregiver + relative duration of time spent with other stimulus). A comparison of the index values from the two types of tests at the same age reveals in which test subjects showed greater preference toward their caregiver. Dogs preferred their caregiver less when the other object was the experimenter, while wolves showed actually no preference toward their caregiver in the presence of an adult dog (paired t-tests). Significant differences are indicated with asterisks (*: p < 0.05, **: p < 0.01).

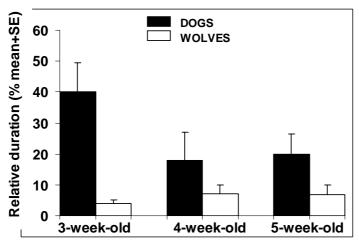


Figure 3.1.1.4.

Mean value (+SE) of relative durations of time spent with vocalization at the age of 3, 4, and 5 weeks averaged the results of the two objectpreference tests. The values of the two species at different age categories were compared by repeated-measures ANOVA. Dogs spent more time vocalizing than wolves, with no effect of age. Significant interaction indicated vocalization tended to decrease with age in the case of dogs, while wolves' vocalization did not change with age.

Tail Wagging

Wolf pups never wagged their tails while approaching the objects for the first time or while first getting into physical contact with them. (Even if we consider the entire period of tests, there was only one pup that showed this behaviour orienting toward the adult dog and also toward the caregiver in one test at the age of 5 weeks. This happened, however, not at the first approach or in physical contact with the objects.) Despite the lack of tail wagging in wolves during the observed periods, the two groups did not differ statistically in the tendency for showing tail wagging in respect of any object at the age of 3 weeks. In the proximity of the nursing bottle and the adult dog, none of the animals showed tail wagging and only few dog puppies (two subjects in the Bottle-Caregiver and three in the Dog-Caregiver test) wagged their tail when approached or contacted the caregiver.

However, 4-and 5-week-old dog puppies significantly differed from wolf pups in case of all objects. Compared to wolves, more 4-week-old dog puppies showed some tail wagging toward the caregiver both in the Experimenter-Caregiver (Fisher exact test; p < 0.001) and in the Pup-Caregiver test (p = 0.029). We found the same species difference in tail wagging in Experimenter-Caregiver test toward the experimenter (p = 0.037) and in the Conspecific Pup-Caregiver test toward the pup (p = 0.029). This difference was also characteristic in case of 5-week-old subjects as dogs wagged their tail more often toward all objects (Dog-Caregiver test: caregiver: p < 0.001; adult dog: p = 0.005, Experimenter-Caregiver test: experimenter: p = 0.001; caregiver: p < 0.001).

Gazing at Face

As we found no difference between the caregiver and the unfamiliar human in respect of gazing at their face (dogs: z = -1.69, p = 0.09; wolves: z = -0.45, p = 0.66 by Wilcoxon test), and considering the relative rare occurrence of this behaviour, we added up the number of gazings at any human face during the tests at a certain age. Three-and 4-week-old animals gazed rarely at the human face, and no difference was found between the species (N(dogs) = 8; N(wolves) = 11; U = 38.50, p = 0.241; N(dogs) = N(wolves) = 11; U = 40.00, p = 0.104, respectively). At the age of 5 weeks, however, dog puppies gazed at the humans' face more often than wolf pups did (N(dogs) = 11; N(wolves) = 12; U = 31.00; p = 0.02) (Figure 3.1.1.5).

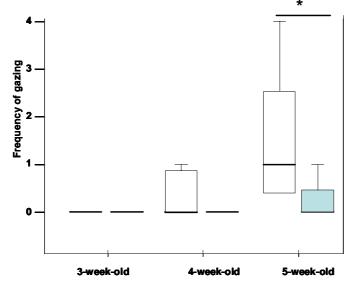


Figure 3.1.1.5.

Frequency (number/min) of gazings at the humans' face in the three age categories during the two tests. The medians of nonparametric data are represented by bold lines, and boxes indicate the 50% of the data (lower and upper interquartile range). Whiskers extend to smallest and largest values excluding outliers extremities. Mann-Whitney U-tests showed that 5-weekold dogs gazed at the

humans' face significantly more frequently than wolves did. Significant differences are indicated with asterisks (*: p < 0.05).

Avoidance

Considering all three age categories together only one dog showed avoidance on 1 occasion (1%) of 98 interactions (taking up the puppy by the experimenter) in contrast to eight wolves displaying such behaviour on 19 occasions (17%) of 106 interactions. Due to the small sample size and the relatively rare occurrence of this behaviour, however, this did not mean significant difference between the species in avoidance shown toward a familiar experimenter at the age of 3 and 4 weeks (Fisher exact test; p = 0.214 and 0.242, respectively) and only a tendency could be demonstrated in case of the 5-week-old pups (p = 0.057).

Aggressiveness

None of the dog puppies behaved aggressively in the 99 interactions with the familiar experimenter during the tests. Among the 13 wolf pups, however, there were nine individuals that one or more times growled at the familiar experimenter and/or tried to bite her (in 29 cases of 112 interactions, 26%). Comparing the species by age-categories, we have found that aggressive behaviour was more pronounced in wolves than in dogs at each age (Fisher exact tests: 3-week-olds, p = 0.04; 4-week-olds, p = 0.013; 5-weekolds, p = 0.001).

3.1.2. EXPERIMENT I/2

METHODS

Subjects

This experiment was carried out only with three dog puppies and four wolf pups, so the results should be regarded as preliminary. Subjects were tested both at the age of 5 and 9 weeks, but most 5-week-old wolf pups fell asleep during the session so only the result of the dogs could be analyzed for this age.

Experimental procedures- Reinforced eye contact test

In case of three dog and four wolf pups, we tried to increase the frequency of eye contact with a familiar experimenter by reinforcing them with food for the required behaviour. The 4-min test sessions were conducted at a familiar place; first, when the subjects were 5 weeks old (after the object-preference tests) and later when they were 9 weeks old. Prior to the test, the incentive value of the food reward was tested by placing small pieces on the floor 1 m from the subject. When we released the subjects, each of them ran to the food and ate it up immediately. Then a familiar experimenter (the same person in all tests) sat on the floor facing the subject continuously. A plate of food (small pieces of cold cut) was placed on a table beside the experimenter out of subjects' reach. The animal could move freely around and when it made eye contact with the experimenter, she signed it with a clicker (a small device that gives a sudden snapping sound when pushed) and immediately threw a piece of food to the animal. If the animal went farther than 1.5 m from the experimenter, she made noise with the plate to redirect its attention. The caregiver sat still 2 m away from the experimenter.

Data recording

The whole session was videotaped. Reviewing the tapes, we counted the number of "clicks," which equalled the number of eye contacts between the experimenter and the animal.

RESULTS

Comparing the number of eye contacts at the age of 9 weeks, no difference was found between the performance of the species in the first minute (t_5 = 0.985, p = 0.370). At the beginning, all animals made intensive attempts to take the food directly from the plate, which was unreachable for them. As the session went on, however, dogs tended to gaze more at the experimenter's face. Wolves, on the contrary, kept mainly orienting toward the plate, even though they always got a food pellet from the experimenter if they happened to gaze at her. Compared to wolves, dogs achieved significantly more eye contact with the experimenter during the fourth minute (t(5) = 4.811, p = 0.005).

To look for any learning effect across the two ages, we compared their performance (difference between number of eye-contact in min 4 and min 1) at the age of 5 and 9 weeks, and found very similar pattern of performance (t(2) = -0.615, p = 0.601) (Figure 3.1.2.1).

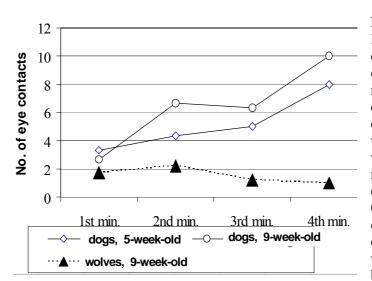


Figure 3.1.2.1.

number of contacts with a familiar experimenter during the 4min long operant conditioning test sessions of dogs at the age of 5 and 9 weeks versus that of 9week-old wolves. (The results of 5-week-old wolves could not be evaluated.) Comparing the number of eye contacts in the presence of a plate with food, 9week-old dogs' and wolves' behaviour did not differ du-

-ring the first minute. During the last minute, however, dogs initiated more eye contacts than wolves. No significant difference was found in the performance of dogs at the age of 5 and 9 weeks.

3.1.3. STUDY I. GENERAL DISCUSSION

Both dogs and wolves in the present study were extensively hand-raised so the main question was whether similar experience in the two species affected their interspecific social attraction in a similar manner.

Wolves preferred the caregiver to the bottle at the age of 3 weeks, which affirms the findings that in some contexts, social stimuli have higher incentive value than food reinforcement for wolf pups (see Frank & Frank 1988). Moreover wolf pups, at the age of 5 weeks (but not at the age of 4 weeks) showed a clear preference for their human "parent" over the unfamiliar human. It could be assumed that the unfamiliar human, being a novel social agent, evoked exploratory behaviour on the part of the 4-week-old wolf puppies. Thus they showed no preference for the caregiver at the age of 4 weeks but it emerged 1 week later when the test was repeated and the other human had lost its 'novelty value.' An alternative explanation might be that for this time the (relatively) novel stimulus may evoke some fearfulness besides the exploratory behaviour in wolf pups. Interestingly, however, social preference towards the human caregiver was masked when the unfamiliar human was replaced with a canid (adult dog or wolf pup); wolves never preferred their "foster parent" in these situations.

Dogs displayed preference for the human caregiver starting from the 4th week, and this preference disappeared only in the last test when they were tested with two humans. This could suggest that dogs, unlike wolves, develop a preference toward humans as they get older, and additionally this preference is not restricted to the caregiver but becomes more generalized by the age of 5 weeks. It is also possible that dog puppies are more sensitive to being "ignored" by their motionless caregiver than are wolf pups, thus are more prone to seek contact (try to initiate social interaction) also with the experimenter.

Taken together, this suggests that both species are able to learn about its heterospecific (human) foster parent but there might be differences in the ability to generalize its characteristics to other similar "objects". If we assume that such recognition (or social attraction) is based on learning a set of features of the parent then the difference may be that wolves are more restrictive in their choice when the caregiver is highly different from the natural parent. While the recognition of a "wolf-like" parent seems to be the "default" state of wolves' learning system, domestication might have changed this in dogs by making the recognition process less precise, that is, recognition can occur in greater ranges of these characteristic features.

It is also important to note that in the case of some communicative signals, further species differences were observed. Dogs vocalized more during the tests that could be the result of a decreased threshold for the elicitation of distress calls in dogs, which is supported generally by the observation that dogs are more vocal in comparison to wolves (Fox 1971). Moreover wolf pups showed more avoidance and aggression toward a familiar human, though the observed difference in such responses might be not unique to interactions with humans. The greater number of growls and attacks (e.g., attempted biting) in wolves and the absence of these behaviours in the case of dogs could be best explained by supposing that wolves either did not like to be touched or constrained in their movements, or they had a lower threshold for the elicitation of aggressive behaviour.

Although tail wagging is listed as a behaviour unit in the ethogram of the wolf (McLeod 1996; Zimen 1987), we found tail wagging only in the dogs during the

observed periods. It seems that dog puppies are either more prone to show submission toward passive social stimuli at the age of 4–5 weeks, or may use tail wagging for a somewhat broader communicative intention to facilitate interaction. The high position of their tail during tail wagging seems to give some support to the latter explanation. It is also interesting to note that tail wagging became also more frequent in the foxes selected for tameness (Belyaev 1978).

Further differences were found in relation to gazing behaviour toward humans. Despite extensive socialization with humans, wolves seem to avoid looking at the face of the experimenter, which was revealed in the low frequency of gazing in the object-preference tests. Their behaviour in the eye contact test 4 weeks later supports the idea that this difference cannot be explained simply by a delay in the development of their social communication system. As wolves proved to be motivated by the food when they could get it for "free" prior to the eye contact test at both ages, we suggest that their reaction could be explained by the strategy observed in wolves in other situations as well when responding to "unsolvable" problems they first tried on their own and then gave up and had a rest (Miklósi et al. 2003).

In the conditioning test, the required behaviour was a very simple one and food reinforcement always followed the eye-contact right away. There are two possible explanations for increased tendency to gaze at the human's face in dogs; either they learned the association between eye-contact and food reward very quickly, or they might not have learned much, but in this moderately stressful situation, they looked more into the human's eyes only because "solicitation" came more natural to them. In the first case, the difference in the performance could stem again from two factors; looking into the eyes of a human can be less "convenient" behaviour for wolves, or there might be some other type of learning difference between the two species in this situation (i.e., dogs were simply more quick in this conditioning task). However, comparative studies on the problem solving abilities and species-specific constraints on learning in the two species have revealed no inferior performance of wolves (Frank & Frank 1985, 1988; Frank et al. 1989).

These results raise the possibility that dogs have been selected for being more resistant to gazing and/or they have been selected for gazing preferentially at humans. Comparative investigations (Frank & Frank 1985; Miklósi et al. 2003) seem to support the latter view when noting that increased gazing at humans could pave the way for the emergence of complex social skills in dogs that are able to utilize this visual communicative channel used predominantly by our species.

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3.2. STUDY II. INFANT-LIKE PATTERNS OF ATTACHMENT BEHAVIOUR IN DOGS BUT NOT IN WOLVES.*

Abstract

Using the Strange Situation Test originally developed for testing the mother-infant relationship in humans, we have compared the attachment behaviour of extensively socialized (hand-reared) dog (*Canis familiaris*) and wolf (*Canis lupus*) puppies toward their human caregiver to pet dog puppies of the same age. The experiment was designed to study (I) whether dog puppies as young as 16 weeks show attachment to a human caregiver (II) whether extensive socialization by human caregivers affects attachment behaviour of dog puppies and (III) whether evolutionary changes (in the form of species-specific differences between wolf and dog pups) play a role in emergence of dog-human attachment.

Results show a characteristic selective responsiveness to the owner in young dogs that is similar to that observed in adults, and this supports the view that already puppies display the patterns of attachment toward their owner. Additionally, we have found that extensive socialisation had only a minor effect on the attachment behaviour in dog puppies as the behaviour of pet dogs and hand-reared dogs was basically similar.

However, we have found significant species-specific difference between wolves and dogs because both extensively socialized and pet dog puppies exhibited highly different responsiveness toward the owner in comparison to an unfamiliar human participant, in contrast to extensively socialized wolves. Behavioural differences could be best explained by assuming that selective processes took place in the course of domestication (genetic changes) that are related to the attachment system of the dog.

Topál J, Gácsi M, Miklósi Á, Virányi Zs, Kubinyi E, Csányi V. (2005). The effect of domestication and socialization on attachment to human: a comparative study on hand reared wolves and differently socialized dog puppies. Animal Behaviour 70(6): 1367-1375.

^{*}Based on:

INTRODUCTION

One of the basic behavioural phenomena of the social relationships is attachment. The evolutionary approach to function and mechanism suggests that attachment is one of the main behaviour organizing systems in parent-offspring relationships, and is also claimed to be the basic organizational factor for any species' social structure leading to group formation (Bowlby 1958). Attachment is an asymmetrical social relationship between two individuals, which can be experimentally tested in choice situations like the Strange Situation Test (SST) originally developed to study the mother-infant relationship in humans (Ainsworth & Wittig 1969). The paradigmatic element of this procedure is that separation from the caregiver in an unfamiliar environment evokes anxiety (which is behaviourally manifested in proximity seeking), whilst the activated attachment system upon reunion with the caregiver manifests in different forms of contact seeking behaviours. Importantly, attachment behaviour is oriented mainly toward the caregiver, in the sense, that there is a significant difference in the level of proximity and contact seeking and efforts for the maintenance of contact between the caregiver and an unfamiliar person in the same novel situation.

Earlier we have reported that adult dogs show specific patterns of attachment behaviour towards their owner in the SST (Topál et al. 1998; Gácsi et al. 2001). Others also found this procedure to be a valid method for assessing dogs' attachment behaviour (Palmer & Custance 2008) pointing to the functional similarities between dogs' and human infants' behaviour in the SST (see also Prato-Previde et al. 2003). Although one could assume that the ability to show attachment behaviour to the individuals of another species (human) in adulthood is one of the unique features of the domestic dog, despite much interest (Scott 1992; Ginsburg & Hiestand 1992), there has been no clear theory explaining the emergence of the phenomenon. Regarding the question whether inheritance (genetic background) or environmental effects (rearing history) plays the more influential role the following two hypotheses can be formulated:

The *Socialization hypothesis* suggests that attachment could develop mainly as a result of the extensive hand-rearing and individual socialization to the human social environment (i.e. enculturation) during the "critical period" of socialization (Freedman et al. 1961).

The *Domestication hypothesis*, however, claims that there could have been specific genetic changes (in the attachment behaviour organizing system) that have emerged as the result of selective breeding for dependency and attachment to humans (see also Hare et al. 2002; Miklósi et al. 2003 for similar explanations regarding communicative abilities in dogs).

In this paper we have designed a comparative experiment to investigate the attachment behaviour of hand-reared and extensively socialized wolf- and dog puppies and pet dog puppies who received usual socialization regimen by their owners. We wanted to seek evidence (I) whether pet dogs' attachment to human is observable in Strange Situation Test as early as 16 weeks of age (II) whether extensive socialization by human caregivers causes any change in attachment behaviour of dog puppies and (III) whether there are species-specific differences between wolves and dogs in their attachment behaviour to human.

The *Socialization hypothesis* predicts that hand-reared wolf and dog puppies will show similar forms of attachment behaviour to their human caregiver whilst pet dog puppies being less extensively socialized will perform less explicit manifestation

of attachment to their owner. In contrast, according to the *Domestication hypothesis* we expect species-specific differences in the attachment behaviour to human between wolves and dogs reared in the same way (i.e. dogs should show more specific attached behaviour toward human than wolves). We should note that these explanations are not mutually exclusive and both of the hypothesized mechanisms could affect the behaviour phenotype in interaction.

3.2.1. EXPERIMENT II/1

METHODS

Subjects

Three experimental groups, a group of extensively socialized wolf puppies and two groups of dog puppies with different rearing conditions were observed in the Strange Situation Test.

Hand-reared puppies

Subjects in the 'hand-reared wolf' (N = 13) and 'hand-reared dog' (N = 11) groups were the same as in the above study (STUDY I). They were 4 months old at the time of testing (mean age \pm SD; wolves: 16.2 ± 0.5 ; dogs: 16.3 ± 0.5 weeks).

Pet dog puppies

Eleven pet dog puppies of different breeds (7 males, 4 females; two mongrels, one-one Border collie, Cairn terrier, Cocker spaniel, Cavalier King Charles Spaniel, German shepherd, Golden retriever, Husky, Moskow Ovcarka, Spitz) were also tested. All of them were raised by their mothers until 7-9_weeks of age, and at the time of the test_they lived in human households and their mean age (\pm SD) was $16.3(\pm2.5)$ weeks.

Experimental procedures

The Strange Situation Test used here for studying dog/wolf-human attachment is based on the subject's differential reaction to the owner and an unfamiliar person (stranger) in a moderately stressful environment. The test procedure was identical to that of reported earlier (Topál et al., 1998; Gácsi et al., 2001). A 5.5 m X 3.5 m enclosure with 2 m high, opaque sidewalls was used as testing facility. The owner and the stranger (both females) entered and left through a 90 cm x 2 m door. There were two chairs placed 1.5 m from each other in the middle of the experimental area (one for the owner and one for the stranger). There were some toys in the otherwise empty place as well. The test procedure consisted of seven episodes, each lasting two minutes. Human participants had to follow a detailed protocol that determined the form and timing of their behaviour. The behaviour of the subjects was videotaped and analyzed later.

Episode 1 (owner and dog/wolf): The owner entered the enclosure together with the dog/wolf, sat down and started to read. After 1 min. she started to stimulate playing or petting the dog/wolf depending on its willingness. (She stopped playing or petting when the stranger entered.)

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Episode 2 (owner, stranger and dog/wolf): The stranger entered, greeted the owner, stopped for up to 5 sec. to allow the animal to respond, and then sits down. After 30 sec. she initiated conversation with the owner. Another 30 sec. later the stranger started to stimulate playing or petting the dog/wolf depending on its willingness. At the end of the episode the owner left as unobtrusively as possible leaving the leash on her chair.

Episode 3 (stranger and dog/wolf): In this first separation episode the stranger tried to play with the animal or offered petting. After 1 min. she sat down and petted the dog/wolf if it was close enough.

Episode 4 (owner and dog): In this first reunion episode the owner called the puppy while she approached the closed door. After entering she stopped for max. 5 sec. to allow the animal to respond and then went to the chairs. Then the stranger left. The owner stimulated playing or petting the dog/wolf depending on its willingness for 1 min., and then sat down and petted the puppy if it was close enough. At the end of the episode she told the puppy 'I must go, you should stay here" and left.

Episode 5 (dog/wolf alone): This was the second separation episode (Total separation). Dogs/wolves were kept in the enclosure for 2 minutes.

Episode 6 (stranger and dog/wolf): The stranger entered and stopped for max. 5 sec. to allow the dog/wolf to respond and then stimulated playing or petting the animal depending on its willingness. After 1 min. she sat down and petted the animal if it was close enough. She stopped playing and petting when the owner entered.

Episode 7 (owner and dog/wolf): In the second reunion episode the owner called the animal while she approached the closed door. After entering she stopped for up to 5 sec. to allow the animal to respond and then went to the chairs. Then the stranger left. The owner stimulated playing or petting the dog/wolf depending on its willingness for 1 min. and then sat down and petted the puppy if it was close enough.

Data collection and analysis

On the basis of the detailed behaviour analysis of two samples of dogs in former two studies (N=51 in Topál et al., 1998 and N=60 in Gácsi et al. 2001) seven variables were recorded. Proximity seeking upon separation was determined by 'Following' of the departing person (owner/stranger) and by 'Standing by the door' when the owner/stranger was absent. Contact seeking behaviours upon reunion were described by scores of 'Contact seeking' towards the entering person (owner/stranger) and by measuring the duration of 'Physical contact' while greeting the owner/stranger. Further, we also measured the duration of the behaviours related to other aspects of the social and physical environment as 'Playing' with the owner/stranger, 'Exploring' the environment in the presence of the owner/stranger and 'Passivity' in the presence of the owner/stranger.

Each behaviour category was coded in the presence of both the owner and the stranger. The detailed definitions of the behaviour categories were as follows:

- 1. Exploration (in the presence of the owner and stranger): Any activity directed toward non-movable aspects of the environment, including sniffing, distal visual inspection (staring or scanning), close visual inspection or oral examination.
- 2. Passive behaviour (in the presence of the owner and stranger): Time spent with sitting, standing or lying down without any orientation toward the environment.
- 3. Playing (in the presence of the owner and stranger): Any vigorous toy- or social partner-related behaviour including running, jumping, or any physical contact with toys.

- 4. Stand by the door (in the presence of the owner and stranger): The time spent close to the door (<1m) with the face oriented to the exit. The behaviour of the animals was always categorised in one of the above four variables during the episodes (non-overlapping behaviour categories).
- 5. Physical contact (with either the owner or the stranger): The amount of time spent in any form of bodily contact.
- 6. Following (the owner and stranger): The tendency to follow the person leaving the kennel was evaluated by using exclusive conditional scores. The puppy did not orient towards the leaving person at all, or only for less than 1 sec (score: 0); it oriented towards the leaving person for more than 1 sec (score: 1); it followed the leaving person to the door (score: 2); it tried to get through the door or stood by the door for more than 1 sec (score: 3). Following was recorded only when one person stayed with the puppy while the other left the enclosure, as it happened at the beginning of episode 3 with the owner, and at the beginning of episodes 4 and 7 with the stranger. (Mean of the scores for the stranger were calculated.)
- 7. Greeting (the owner and stranger): The behaviour of the dog toward the entering owner or stranger was evaluated by using the following five criteria, and summing up the scores.

approach initiation (+1): the puppy moved toward the entering person;

full approach (+1): the puppy approached the entering person until getting into physical contact;

avoidance (-1): any sign of avoidance behaviour toward the entering person, e.g. backing, getting out of the way of the entering person;

durable physical contact upon greeting (+1/2): the puppy spent more than 3 seconds in bodily contact with the entering person;

delay of approach (-1/2): when the owner/stranger enters, the puppy hesitated to initialize any approach for more than 5 seconds.

(The maximum score was 5 with the respect to both the owner/caretaker and the stranger, because both of them entered the enclosure twice.)

We calculated the relative percentage of the time spent in Exploration, Playing, Passive, Stand by the door and Physical contact. All variables passed normality test (Kolmogorov-Smirnoff) therefore we applied parametric statistical methods (SPSS version 9.0). We analysed the behaviour of puppies in presence of the owner and stranger (within subject factor) and the experimental group (between subject factor) with mixed ANOVA for repeated measures to the within subject factor. Further, we used Sudent-Newman-Keuls post hoc tests (between groups comparisons) and paired t-tests (within group comparisons).

Before data analysis interobserver agreements for all of the seven behaviours were assessed by means of parallel coding of the 50% of the whole sample. We calculated Kappa coefficients (Martin & Bateson 1986) and found relatively high values for all variables (Exploration: 0.773, Playing: 0.964, Passive: 0.810, Stand by the door: 0.909, Physical contact: 0.881, Following: 0.721). In order to assess the interobserver agreement for Greeting, we measured Kappa coefficients for latency to approach (0.875), avoidance (0.880) and time spent in physical contact upon greeting (0.987).

RESULTS

Regarding the behaviour observed in the presence of the owner and stranger first we give a short description of the experimental groups. "In the presence of the

stranger" always refers to those episodes in which the stranger was present (episodes 2, 3, 6) while those episodes in which the caregiver (owner) was present (episodes 1, 2, 4, 7) were labelled as "in the presence of the owner".

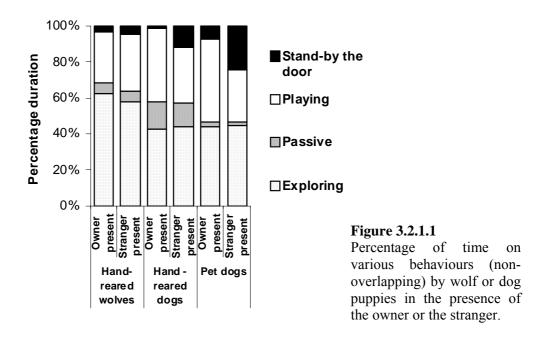
Behaviour of hand-reared wolf puppies

In the unfamiliar situation subjects spent most of their time exploring the environment (62.6% in the presence of the owner and 57.7% in the presence of the stranger) and playing (28.7% of the total duration with the owner and 31.5% with the stranger). In contrast, they spent hardly any time on passive behaviours (5.6% when the owner was present and 5.9% when the stranger was present) and or on standing by the door (3% and 4.8% of the total duration in the presence of the owner and stranger). (Figure 3.2.1)

Wolves seemed to prefer physical contact with the stranger (21.4% of the total time) than with owner (8.8%) and were ready to follow both of them (Figure 3.2.2). They obtained relatively high mean scores of greeting towards the entering owner and stranger as well (see Figure 3.2.3). In total separation (episode 5), when the subject was alone in the enclosure wolves spent most of their time with exploring the environment (36% of the total duration) and stood by the door (55% of the total duration).

Behaviour of hand-reared dog puppies

Like wolves, extensively socialized dog puppies also played a lot with the human participants (41% with the owner and 30.7% with the stranger) and explored the environment thoroughly (42.8% and 43.7% of the total duration in the presence of the owner and stranger). They spent more time being passive (14.7% and 13.5%) than wolves, and they stood by the door less when owner was present (1.38%) than in the presence of the stranger (12.02%, Figure 3.2.1.1). They tended to follow and greet the owner more than they did with the stranger (Figures 3.2.1.2 & 3.2.1.3). In episode 5 (when they were alone) hand-reared dogs spent a lot of time standing by the door (43.5%) and exploring the environment (39% of the total duration).



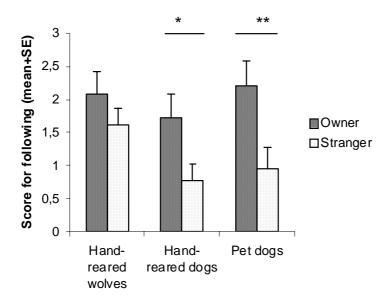


Figure 3.2.1.2.

Mean scores +SE (range 0-3) for following the owner and stranger when she left the test room (averaged over episodes 2, 4 and 3, 6 respectively). Paired t-test, *: p < 0.05, **: p < 0.01

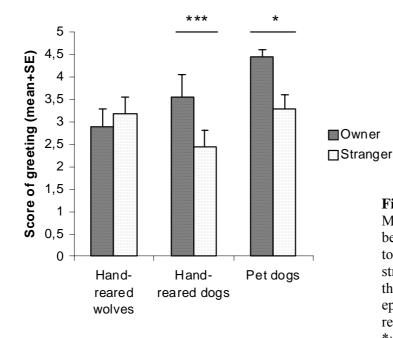


Figure 3.2.1.3.

Mean scores of greeting behaviour (maximum 5) towards the owner and stranger when she entered the test room (averaged over episodes 4, 7 and 2, 6 respectively). Paired t-test, *: p < 0.02, ** p < 0.002

Behaviour of pet dog puppies

Pet dogs also showed a lot of exploration (43.9% when owner was present and 44.7% in the presence of the stranger) and little passive behaviour (2.5% and 2.2%). They showed some preference for playing with the owner (46.1% of the total duration vs. 29.1% in the presence of the stranger) and stood by the door less when the owner was present (7.5% vs. 24%, Figure 3.2.1.1).

However, pet dogs spent similar times in physical contact with the owner (11% of the total duration) and stranger (14.1%). As with hand-reared dogs, we observed a significant asymmetry regarding greeting and following behaviours (higher greeting and following scores with the owner – see Figures 3.2.1.2 & 3.2.1.3). In the total separation episode pet dogs either explored the environment (59%) or stood by the door (41% of the total duration).

Between-group comparisons

Exploring the environment: The groups showed significant differences (wolf puppies explored more than dogs; F(2,33) = 3.41, p = 0.045), but neither the within subject factor (i.e. exploration in the presence of the owner vs. stranger) nor the interaction proved to be significant (F(1,32) = 0.21, p = 0.65 and F(2,33) = 0.71, p = 0.50 respectively). Paired comparisons of the exploration in the presence of the owner vs. stranger failed to show significant differences in any of the groups (wolves: t(12) = 1.51, p = 0.15, hand-reared dogs: t(10) = 0.49, p = 0.63, pet dogs: t(10) = 0.12, t(10) = 0

Passive behaviours: Two way ANOVA showed significant differences between groups (hand-reared dog puppies spent more time with passive behaviours than wolves and pet dogs; F(2,33) = 4.84, p = 0.015. In contrast, the within subject factor (i.e. passive behaviours in the presence of the owner vs. stranger) and the interaction were not significant (F(1,32) = 0.13, p = 0.72 and F(2,33) = 0.17, p = 0.84 respectively). In agreement with this, within group comparisons did not show differences in passive behaviours with owner vs. stranger (wolves: t(12) = 0.42, p = 0.67, hand-reared dogs: t(10) = 0.46, p = 0.65, pet dogs: t(10) = 0.17, p = 0.87).

Physical contact with owner/stranger: Wolf puppies spent more time in close bodily contact with their human partner than hand-reared dog puppies whilst the behaviour of the pet dog group was intermediate (between group effect: F(2,33) = 3.99, p = 0.028). Within subject factor was also significant (physical contact with the owner vs. stranger: F(1,32) = 8.67, p = 0.006) but interaction was not F(2,33) = 1.56, p = 0.23. Interestingly, both hand-reared dogs and wolves had more bodily contact with the stranger than owner (f(10) = 2.85, f(10) = 0.017, and f(12) = 2.52, f(10) = 0.027) while similar differences were not found in pet dogs (f(10) = 0.72, f(10) = 0.72).

Playing: The groups did not show significant differences in play (F(2,33) = 0.39, p = 0.68); however both the person present (i.e. owner or stranger) and the interaction were be highly significant (F(1,32) = 18.83, p < 0.0001 and F(2,33) = 10.02, p < 0.0001, respectively). Both hand-reared and pet dogs but not wolf puppies tended to play more with their owner than with the stranger (hand-reared dogs: t(10) = 3.75, p = 0.004, pet dogs: t(10) = 5.13, p < 0.0001, wolves: t(12) = 0.81, p = 0.43).

Following the owner/stranger: The analysis of the subjects' reaction to the person going away failed to show differences between groups (F(2,33) = 1.30, p = 0.29) whereas the within subject factor was highly significant (F(1,32) = 16.73, p < 0.0001). We did not find significant interaction in this case (F(2,33) = 1.16, p = 0.34). Within group comparisons show that while wolves did not discriminate between humans in this case (owner vs. stranger: t(12) = 1.2, p = 0.26), both pet and handreared dog puppies were more ready to follow the owner than stranger (t(10) = 4.03, p = 0.002) and t(10) = 2.35, p = 0.041).

Standing by the door: Two-way ANOVA showed significant effects for both the comparisons between groups (F(2,33) = 3.86, p = 0.031; pet dogs stood more at the door than hand-reared dogs or wolves) and within subjects (F(1.32) = 21.96, p < 0.0001). The interaction was also significant (F(2,33) = 4.54, p = 0.018). Hand-reared and pet dogs spent more time standing by the door when the owner was absent

versus present (t(10) = 2.77, p = 0.020 and t(10) = 3.25, p = 0.009 respectively), in contrast to wolves (t(12) = 1.38, p = 0.19).

Greeting the owner/stranger: The subjects' greeting behaviour toward the entering owner and stranger did not show significant differences between groups (F(2,33) = 2.07, p = 0.14). However, the identity of the entering person (within subject factor: F(1,32) = 8.13, p = 0.008) and interaction (F(2,33) = 4.62, p = 0.020) proved to be significant. Paired comparisons of the greeting behaviour showed that while dogs of both groups greeted more intensively the owner than the stranger (pet dogs: t(10) = 2.85, p = 0.017, hand-reared dogs: t(10) = 4.35, p = 0.001) wolves did not make such discrimination (t(12) = 0.61, p = 0.55).

Behaviour in the total separation: Subjects in all groups spent episode 5 (subject alone) mainly with exploring the enclosure (in average 44.7% of the total duration) or standing by the door (in average 46.5% of the total duration). Between group comparisons showed no significant differences for exploration (F(2,32) = 1.11, p = 0.34) and standing by the door (F(2,32) = 2.66, p = 0.085). The increased durations (41-55%) of standing by the door when subjects were alone in the enclosure (in other episodes dogs and wolves stood by the door for 1.4-24% respectively) clearly show that puppies in all groups found this episode distressing. This is also supported by the fact that almost all puppies (all hand reared dogs and all but one wolf and pet dog) followed the leaving person when they were left alone (which meant they got the maximum score for following at the end of episode 4).

3.2.2. STUDY II. GENERAL DISCUSSION

In agreement with earlier studies, which suggested that adult pet dogs (Topál et al. 1998) and adult shelter dogs after a short handling procedure (Gácsi et al. 2001) show patterns of attachment behaviour toward the owner/handler, our results suggest that this behaviour can be evoked in dog puppies as early as 16 weeks after birth. Table 3.2.1.1. summarizes the paired comparisons of the behavioural variables in the presence of the owner and the stranger and gives further support for this conclusion.

Traditionally fostered four months old dog puppies showed in most respects the same discrimination between human participants (owner versus stranger) as adult pet dogs did in our earlier study (Topál et al. 1998). This suggests that the attachment behaviour system is activated upon separation from the owner but not the stranger (standing by the door upon separation and following the owner who is leaving the enclosure), and upon reunion with the owner (increased proximity and contact seeking). This characteristic selective responsiveness to the owner supports the view that both adult dogs and puppies show the same patterns of attachment toward their owner.

Our findings strongly argue for a small influence of intensive socialisation in dogs on attachment to human caregiver as both hand-reared and pet puppies selectively responded to the separation from the owner. Results show only minor effect of the socialization history: pet dog puppies spent more time with passive behaviours than hand-reared ones, whereas hand reared puppies spent more time close to the door and showed a stronger preference for physical contact with the stranger. The greater interest in unfamiliar human could be an artefact of hand-rearing as this was the only apparent feature that was typical for both hand-reared

groups (dog and wolf puppies). In fact, due to their special socialization, hand-reared pups had more extensive experience with different unfamiliar humans (strangers) during their first months than pets.

GROUP	Score of contact seeking	Physical contact	Stand by the door	Follo- wing	Playing	Passive	Explo- ring
Pet dog puppies (N=11)	O > S p=0.017	p=0.487	O < S p=0.009	O > S p=0.002	O > S p=0.001	p=0.870	p=0.904
Hand- reared dog puppies (N=11)	O > S p=0.001	O < S p=0.017	O < S p=0.019	O > S p=0.041	O > S p=0.004	p=0.655	p=0.631
Hand- reared wolf puppies (N=13)	p=0.551	O < S p=0.027	p=0.192	p=0.255	p=0.432	p=0.677	p=0.156
Adult pet dogs* (N=51)	O > S p<0.001	p=0.131	O < S p<0.001	Data not availabl e	O > S p<0.001	p=0.145	O > S p=0.013

Table 3.2.1.1. Summary of the paired comparisons of the behavioural variables in the presence of the owner (O) versus the stranger (S) *The data for adult dogs are taken from Topál et al. (1998); p values are from paired t tests.

Importantly however, the present study shows, that species-specific difference in attachment behaviour toward humans exists between hand-reared dog and wolf puppies. Whilst socialized wolf pups did not show the specific patterns of attachment (person-specific proximity seeking upon separation and contact seeking upon reunion, see Table 3.2.1.1), this behaviour mechanism is unequivocally activated in 16 weeks old dog puppies. Additionally, even socially deprived adult dogs display such attachment behaviour after a short social handling of an unfamiliar person (Gácsi et al. 2001).

These results provide little support for either the attachment to humans being the outcome of extensive human socialization or processes related to heterochronic changes in rates of behaviour development alone (Coppinger & Coppinger 2001; Goodwin et al. 1997). This is in contrast to widely held views as up to now both processes have been implicated heavily in explaining the development of dog-human attachment. Such theories have assumed that the behaviour of dogs shown toward the owner is derived directly from the puppy-mother relationship in wolves, supposing a behavioural homology between dog and wolf behaviour.

Regarding the wolf pup attachment behaviour to mother many observed that the pups' proximity and contact seeking behaviour towards their mother gradually decreases after weaning (6-8 weeks of age –Mech 1970) and social attachment could be observed mainly towards the pack and not a specific individual (King 1954; Rabb et al. 1967; Beck 1973). Sixteen-week-old wolves are often left alone at a "meeting point" where they are waiting for the hunting group (Mech 1991). It has also been reported that in case of 2 months old dog puppies the mother has only minor role in

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reducing the effect of separation stress (Elliot & Scott 1961; Frederickson 1952; 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). On the basis of these findings many questioned that puppies are able to show attachment behaviour to their mother at all despite their ability to discriminate and preference for the mother in certain situations (Rajecki 1978).

In line with these results we suggest that there is no direct functional relationship between puppy-mother attachment in wolves and the life-long behaviour phenomenon that can be called attachment between dog and its owner. Based on our results the most plausible hypothesis is that besides a destabilizing selection (Belyaev 1979) that resulted in the fragmentation of the well-organized behaviour repertoire of the wolf, dogs have evolved a capacity for attachment to human that is functionally analogous to that present in human infants.

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3.3. THE SOCIALITY DOMAIN OF DOG BEHAVIOUR COMPLEX: SUMMARY OF RESULTS.

The comparative analysis of subjects' behaviour toward human participants in the different experimental situations show that even after extensive socialization wolves display increased defensive aggression and this indicates a lower threshold for socially inflicted constraints. Moreover, hand-reared wolves do not display early-emerging and generalized preference toward human as well as patterns of attachment to humans comparable to that observed in pet dog puppies of different rearing conditions. Dogs' attachment to humans is grounded on a specific behaviour organising mechanism while this "software" is seemingly lacking in wolves.

These characteristics of social-affiliative behaviour system in dogs do not only allow for developing close relationship to a different species but also operate for an extended period into adult life (e.g. Topál et al. 1998). This system could also serve as the scaffolding on which many forms of complex social behaviour between dogs and humans can develop (see also Gácsi et al. 2009).

In parallel to other dog-wolf comparisons (Miklósi et al. 2003), these findings give rise to the notion that specific selective processes (genetic changes) might be associated with the emergence of the "sociality" component of the Dog Behaviour Complex. Thus the results of STUDY I & II lend support to the domestication hypothesis which claims that in dogs, due to selection for dependency and attachment to humans, specific genetic changes in the social-affiliative behaviour system have emerged and these changes served as the basis of the evolutionary development of dog-human relationship.

Our observations also point to clear and testable behavioural differences between the results of a socialization process (often referred to as "taming") and the effects of domestication that are reflected in adaptive genetic changes. In the case of the dog such genetic changes resulted in a human analogue attachment system that has probably strongly contributed to the successful "adoption" of the dog into the human social system.

We may assume that the development of social attraction and individualized attachment serve as a basis for the dogs' social competence and attachment has an important role in synchronisation of interacting parties as this could make collaborative activities more easily and efficiently.

CHAPTER 4.

SYNCHRONIZATION

Synchronization can be defined as processes leading to behavioural and motivational/emotional conformity. Achieving behaviours related in time (synchrony) is essential for group cohesion (Engel & Lamprecht 1997). Thus the ability for behavioural synchronization probably enhanced the ability of dogs to maintain close relationships with humans. Scant research on the interactional synchrony between dogs and humans has revealed so far four aspects of dog behaviour: (i) complementary cooperation (ii)emotional synchronization, (iii)imitative behaviours and (iv) rule following.

Complementary cooperation: Goals can often be achieved only by cooperative interactions with others in the group. Earlier we have shown that interacting dogs and humans establish a complex behaviour pattern when performing joint actions (Kerepesi et al. 2005). Dogs are not only sensitive to meta-communicative signals (e.g. the play bow) in order to maintain play but also engage in complex "behavioural projects" in order to continue playing (Mitchell & Thompson 1991). More importantly, dogs seem to be able to perform complementing actions to achieve a joint goal (Naderi et al. 2001) and this closely resembles cooperative activity described in the case of humans (Reynolds 1993).

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, Rooney et al. (2001) provided some evidence of synchronization during heterospecific play when various play signals seemed to have the potential to evoke play behaviour from the other, probably through change in mood. In order to gain a deeper insight into this aspect of dog-human synchronization, in the present chapter three experiments (see STUDY III) will focus on the dogs' ability to adjust their own emotional and behavioural response in accordance with the human's attitude.

Imitative behaviours: Like in mother-infant relationships (Stern et al. 1977), the synchronized routines that dogs and their owners often establish could be an important contributor to the formation of social relationship. In line with other studies (Miller et al. 2009) here we show that dogs can use human behaviour as a cue for selecting functionally similar behaviour. STUDY IV in this chapter provides further evidence of dogs' imitative abilities.

Rule following: de Waal (1996) and others assume that obedient behaviour of dogs and their "desire to please us" is partially based on their social skill at comprehending and following social rules (Bekoff & Allen 1998). There is some evidence that dogs are inclined to follow social rules of the group in both the short and long term. In a previous study we found that dogs adopt spontaneously a novel, arbitrary (actually pointless) behaviour as a result of interaction with their owner (Kubinyi et al. 2003). This can be regarded as a simple form of rule following; the individual develops and maintains habitual behaviour 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. In the last experimental study of this chapter (STUDY V) we tested whether dogs' behaviour could be explained in terms of rule following when in an object permanence task.

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4.1. STUDY III. DOGS' SENSITIVITY TO CHANGES IN HUMAN BEHAVIOUR.*

Abstract

Responsiveness of adult pet dogs (*Canis familiaris*) to an unfamiliar human was observed in three experiments. Subjects were faced with an approaching woman (Stranger) who showed definite signs of friendliness and threat during alternate approaches. Observations consisted of two episodes: the Stranger either approached the dog in normal speed of walk while talking to it (Friendly approach) or she moved slowly and haltingly and looked steadily into the eyes of the dog without any verbal communication (Threatening approach).

In the first experiment 30 dogs of different breeds were tested in the two conditions in a balanced sequential order. The dogs acted appropriately according to the different human behaviour cues.

In the second experiment 60 dogs of three breed groups (20 Belgian shepherds, 20 retrievers and 20 sled dogs) were first "greeted friendly" and then "approached threateningly" by the same Stranger. Results show significant breed specific differences in the responsiveness when dogs faced an apparent switch of the human behaviour cues. Compared to retrievers and sled dogs, Belgian shepherds more frequently changed their response, showing passive or active avoidance or sign of aggression when approached threateningly. While sex differences were not found, breed comparisons suggest that selective breeding (i.e. for hunting or shepherd work) influenced the dogs' sensitivity to human social cues in different ways.

In the third experiment we investigated the responsiveness of 23 Belgian shepherds toward the Stranger, repeating the test at least six months later. The consistency of the dogs' response was found to be moderately high. This procedure proved to be reliable enough to be a valuable measure of a definite part of the personality characters of dogs. Results also support the hypothesis that human influence (domestication) has led to extreme flexibility of the dogs' situation-relevant behaviour while interacting with an unfamiliar human.

*Based on:

Vas J, Topál J, Gácsi M, Miklósi Á, Csányi V. (2005). A friend or an enemy? Dogs' reaction to an unfamiliar person showing behavioural cues of threat and friendliness at different times. Applied Animal Behaviour Science 94: 99-115.

Vas J, Topál J, Győri B, Miklósi Á. (2008). Consistency of dogs' reactions to threatening cues of an unfamiliar person. Applied Animal Behaviour Science 112: 331-344.

INTRODUCTION

Despite the fact that dog trainers routinely utilize social cues in the course of training, the problem of how these stimuli are functioning in dog—human interactions has received relatively little attention. When the role of social cues in dog—human interaction is studied, we should consider that present dogs are the result of a special behavioural evolutionary process called domestication. Wolf—dog comparisons led some to suppose that domestication resulted in the emergence of an unprecedented flexibility of the behavioural system in the dog (Frank & Frank 1987) and this plasticity made it possible for the dog to live in the close proximity to humans. Generally, it seems that compared to their wild ancestors, dogs social interest towards humans is accompanied by relatively greater sensitivity to human behavioural cues (Hare et al. 2002; Frank & Frank 1982; see also STUDY I & II above). In line with this, dogs should show high responsiveness to a broad range of social stimuli from humans and should react very flexibly to the human behaviours expressing different emotional attitudes.

In this study we investigate how dogs are able to modify their own behavioural actions in response to the behavioural changes of a human partner. The first experiment is aimed at the questions whether dogs show corresponding changes in their reactions to an approaching human who shows apparent changes in her behaviour (friendly/threatening).

4.1.1. EXPERIMENT III/1.

METHODS

Subjects

Thirty pet dogs of 19 different breeds and five mongrels were involved in the present study on the basis of their owners' volunteer participation. All subjects were adults (aged between 1-10 years) and half of them were females. For the observations dogs were divided in two groups.

'First-Greeted' group

Fifteen individuals (5 males, 10 females; 2-2-2 German shepherds, Hungarian vizslas, Belgian shepherds, 1-1 Miniature poodle, Cocker spaniel, Beagle, Border collie, Briard, German hunting terrier, Welsh terrier, Fox terrier and a mongrel; mean age±SE: 3.5±3.1 years) were tested first in the 'Friendly approach' episode.

'First-Threatened' group

Fifteen individuals (10 males, 5 females; 1-1 German shepherd, Miniature poodle, Cocker spaniel, Airdale terrier, Boxer, Belgian tervueren, Hovawart, Great dane, Pumi, Rottweiler, Shar-pei and four mongrels; mean age±SE: 2±1.3 years) started with the 'Threatening approach' episode.

Experimental procedures

Behavioural observations were made at a visually separated location in a park near a dog training school, which was familiar to the dogs. Three participants, the dog, the owner and a young unfamiliar woman (Judit Vas – Stranger) took part in the observations. The behaviour of the dog was recorded from the side by another person (cameraman) from a greater distance (10 m). The owner was asked to tether his/her dog with a 1.5 m long leash to an isolated tree and to make it sit or lie down (depending on the dogs controllability) orienting towards the Stranger who stood motionless 5 m from the dog. Then the owner stepped back to a predetermined point (about half a meter behind the dog) and stayed there without moving or speaking.

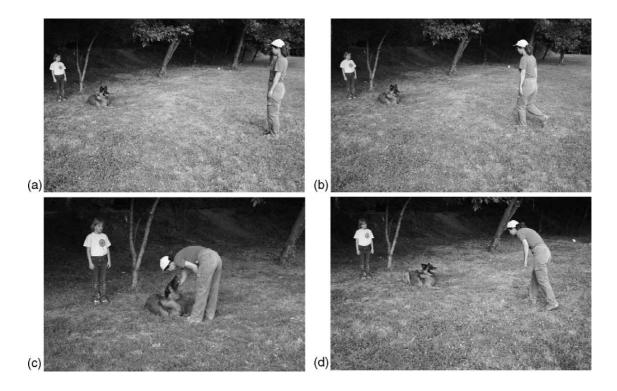
The test consisted of two subsequent episodes (Friendly approach and Threatening approach). The dogs were observed first in either of the episodes. At the end of the first episode the Stranger returned to her starting position (5 m away from the dog). The owner got the dog to its initial position (sit/lie down) stepped back again and the second episode started immediately.

Friendly approach

The Stranger stood 5 m away from the dog and called it by its name. When the dog gazed at her face, she started to approach it in normal speed of walk while she spoke in a friendly manner to the animal and tried to keep continuous eye contact with it. If the dog showed explicit signs of fear or aggression (passive or active avoidance, attack, vocalization - in detail see below) she stopped and the trial was terminated. If the dog did not show any of these behaviours she approached the dog and petted it gently (Figure 4.1.1.1 a–c).

Threatening approach.

The unfamiliar woman stood motionless and silently 5 m from the dog. At the moment when the animal looked at her face, she began to approach it. She was moving slowly and haltingly (one step in every 4 s) with slightly bent upper body and she was looking steadily into the eyes of the dog without any verbal communication (Figure 4.1.1.1 d).



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The behaviour of the Stranger was determined and standardized across subjects according to the following 'If ...then...' rules (a-d):

- (a) If the dog kept looking at her, then she continued to approach the dog and finally petted it.
- (b) If the dog interrupted the eye contact with her (moving away and/or turning head away), she stopped and waited motionless for about 4 s and then she tried to attract the dogs attention: she made some noise (had a slight cough or scratched the ground with her foot). If the dog continued to avert his gaze the Stranger attempted to call the dog's attention two more times (with 2 s in between attempts). Whenever the dog looked again at her, the Stranger continued the approach. If, however, the dog did not look at her after the third attempt, the Threatening approach was terminated.
- (c) If the dog showed active avoidance, that is, it moved away to the back of the owner from the approaching Stranger while keeping eye contact, she stopped and Threatening approach was terminated.
- (d) If the dog showed definite signs of aggression, e.g. barked repeatedly or growled continuously (more than 4 s) and/or tried to attack the Stranger (moving ahead and stretching the leash), Threatening approach was terminated. If the subject did not show any form of fear or aggression mentioned even when the unfamiliar woman reached it, she touched the dog's head and gently petted it.

Comparing the two episodes it is important to note that the Stranger attempted to obtain continuous eye contact in both of them. In contrast to the Friendly approach verbal communication cues were absent in the Threatening approach (except for attention getting signals). The speeds of approach of the Stranger were normal speed of walk in the case of the Friendly and slow in the Threatening episode. The body position of the Stranger was erected in the Friendly and slightly bent in the Threatening approach.

Data collection and analysis

The behaviour of the dogs was scored separately in both episodes by using the following definitions:

Moving off

Score 0: The dog does not move away from the approaching Stranger while gazing at her.

Score 1: The dog moves away from the approaching Stranger while gazing at her, but it does not move behind the owner.

Score 2: The dog moves behind the owner while gazing at the Stranger.

Avert gaze

Score 0: The dog is continuously looking at the face of the Stranger or if eye contact is interrupted, the subject re-establishes it again within 4 s.

Score 1: The dog averts its gaze from the Stranger for more than 4 s (i.e. "warning noise" made by the Stranger is needed to re-establish eye contact).

Score 2: The dog averts its gaze from the Stranger and does not look back even after the third 'warning noise' made by the Stranger.

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Vocalization

Score 0: The dog neither barks nor growls.

Score 1: Barking and growling last not longer than 4 s.

Score 2: The dog barks repeatedly or growls continuously (more than 4 s).

Attack

Score 0: The dog does not make any sudden movement towards the Stranger associated with growling or barking or trying to bite.

Score 1: The dog initializes some sudden movements towards the Stranger associated with a short growling or barking response (0–4 s) while still on loose leash.

Score 2: The dog makes some sudden movements towards the Stranger associated with continuous growling or barking (more than 4 s) or attempts to bite while stretching the leash.

Contact seeking

Score 0: The Stranger cannot pet the dog because the trial is terminated before she could reach the dog.

Score 1: The trial is terminated by petting the dog, but when the Stranger reaches out her hand to pet the dog, it does not move towards her or moves towards her without tail wagging.

Score 2: The trial is terminated by petting the dog, and when the Stranger reaches out her hand to pet the dog, it moves towards her while wagging its tail.

Interobserver agreements for all of the five behaviour categories were assessed by means of parallel coding of the total sample by two observers and relatively high values were calculated in all cases (Index of concordance and Kappa coefficient, respectively, are 0.93 and 0.76 for 'moving off', 0.9 and 0.75 for 'avert gaze', 0.95 and 0.84 for 'vocalization', 0.97 and 0.81 for 'attack', 0.93 and 0.84 for 'contact seeking').

For data analysis we used nonparametric statistical methods (SPSS, version 9.0). Mann–Whitney U test was used to compare the scores of the five behaviour variables between experimental groups (*First-Greeted* versus *First-Threatened*), sexes (males versus females) and between the two age groups (1-year-old dogs versus more than 3-years-old dogs). Comparisons between the two episodes (Friendly approach versus Threatening approach) were analysed by Wilcoxon matched-pairs signed rank test. Chi² test of homogeneity and Fisher's exact test were applied when the distribution of the dogs in the main response categories were analysed.

RESULTS & DISCUSSION

Order effect of the Friendly/Threatening approach

Comparisons of the behaviour variables of the two groups (First-Greeted and First-Threatened) did not show any significant differences in the Friendly approach episode ($N_1=N_2=15$; U=105, p=0.77 for 'moving off', 'vocalization' and 'attack'; U=112.5, p=1 for 'avert gaze' and U=106, p=0.81 for 'contact seeking'). When the Stranger approached in a friendly manner, none of the dogs have averted their gaze and only 1-1 dog from both groups showed 'moving off' or 'vocalization' or

'attack' towards the human. In contrast, most dogs in both groups displayed high levels of 'contact seeking' (only 1-1 dogs did not show any contact seeking while seven and six individuals in the two groups received the maximum score for contact seeking).

Results were similar when the behaviours observed in the Threatening approach episode were compared (First-Greeted versus First-Threatened groups). The only difference between the two groups was that dogs in the First-Threatened group tended to avert their gaze more during the Threatening approach in comparison with those who met the friendly behaving Stranger first (N_1 = N_2 = 15; U = 59.5, p = 0.026). None of the other behaviours 'moving off' (U = 126, p = 0.56) and 'vocalization' (U = 92.5, p = 0.41), nor 'attack' (U = 112.5, D = 1) and 'contact seeking' (U = 106, D = 0.81) have shown significant differences.

When the Stranger approached the dog she adapted her behaviour to the dog's reaction: the Friendly/Threatening approach was interrupted and the trial was terminated when the dog either averted its gaze continuously, or moved off actively or showed signs of aggression. Otherwise she fully approached the dog and petted it. As Table 4.1.1.1 shows this differentiation provides an opportunity to categorize the dogs' responses on the basis of their behaviour for the further analysis.

All dogs in both experimental groups were classified into one of the 'passive', 'friendly', 'passive avoidant', 'active avoidant' or 'threatening' categories (Table 4.1.1.2). In the Friendly approach episode almost all dogs in both groups (14-14 out of the 15) showed 'friendly' or 'passive' behaviours, however, when the Stranger approached them threateningly, more than half of them (8 and 9, respectively) avoided the interaction with the Stranger (performed either 'passive/active avoidance' or 'threatening' behaviour). Considering the small sample (less than five individuals) in 13 out of the 20 cells (see Table 4.1.1.2) we could only compare the distribution of the dogs among the main categories ('Seeking for/tolerating' versus 'Avoiding', see Table 4.1.1.1). This analysis, however, showed no significant differences either in Friendly approach or in Threatening approach episode. First-Greeted group versus First-Threatened group in Friendly approach episode: $chi^2(1) = 0.13$, p = 0.71 and in Threatening approach episode p = 1 (in this latter case with Fisher's exact test).

How was the trial terminated?	Full approach: S.	petted the dog.	Interrupted approach: S. did not pet the dog.			
The dog's reaction at the end of the trial	Did not move tail waggingly towards the outstretched hand.	Moved tail waggingly towards the outstretched hand.	Averted its gaze continuously.	Moved toward the O. or behind the O. while gazing at the S. (and/ or vocalizing)	Made sudden movement toward the S. and vocalizing (stretching the leash)	
Response categorization	passive	friendly	passive avoidant	active avoidant	threatening	
	Seeking for/tolerating the interaction with the S.		Avoiding the interaction with the S.			

Table 4.1.1.1 Categorizing the dogs' response to the Stranger. (Note: S= Stranger O= Owner).

		CATEGORIES					
		Seeking fo	or/tolerating the	Avoiding the interaction			
		interaction with the S.		with the S.			
Episodes		passive	friendly	passive avoidant	active avoidant	threatening	
	Friendly	8 (6, 2)	6 (3, 3)	0	1 (1, 0)	0	
First-greeted	approach I.						
group (N=15)	Threatening approach II.	5 (4, 1)	2 (1, 1)	4 (2, 2)	2 (2, 0)	2 (1, 1)	
	1 1 1	2 (0, 2)	2 (2 1)	2 (0, 2)	5 (2, 2)	2 (1 1)	
First- approach I. threatened group (N=15) Threatening approach I. approach II.		3 (0, 3)	3 (2, 1)	2 (0, 2)	5 (2, 3)	2 (1, 1)	
		7 (2, 5)	7 (3, 4)	0	0	1 (0, 1)	

Table 4.1.1.2 Number of individuals (females, males) showing different responsivity to the Stranger in the two episodes.

It seems that the sequential order of the two episodes (i.e. the fact whether Threatening approach was preceded or followed by a Friendly approach of the Stranger) had only minor effect on the behaviour of the dogs. Therefore, the two groups were merged for further analysis in order to study how the dogs adapted to the changes in the behaviour of the Stranger.

Situation-relevant changes in the dogs' behaviour

The question whether the dogs altered their behaviour in accordance with the switch in the Stranger's way of approach was first studied by paired comparisons of the five behaviour variables between Friendly approach and Threatening approach episodes. This analysis shows significant differences for all but one recorded behaviours ($T_{-} = -28$, p = 0.015 for 'moving off'; $T_{-} = -153$, p < 0.001 for 'avert gaze'; $T_{-} = -55$, p = 0.002 for 'vocalization'; $T_{-} = -6$, p = 0.25 for 'attack' and $T_{+} = 246$, p < 0.001 for 'contact seeking'). Dogs tended to move off, avert their gaze and vocalize more in the Threatening approach episode and performed less contact seeking compared to the episode when Stranger approached them friendly.

Changes in the dogs' reactions due to the modifications in the Stranger's attitude (i.e. friendly or threatening) can be further analysed by comparing the individuals' distribution among the five response-categories ('passive', 'friendly', 'passive avoidant', 'active avoidant' and 'threatening') in the two episodes. This analysis showed a highly significant difference $chi^2(4) = 18.6$, p = 0.001). Namely, when the Stranger greeted them in a friendly manner almost all individuals were scored as 'friendly' (13/30) or 'passive' (15/30) in contrast to the Threatening approach episode when only the minority of dogs responded 'friendly' (4/30) or 'passively' (9/30) and many of them (17/30) were categorized as Avoiding the interaction with the Stranger.

Analysing the behaviour of the dogs in its continuity across the two episodes (Friendly approach and Threatening approach) individuals could be assigned to four main categories (Table 4.1.1.3).

	Threatening Approach episode				
	Response Categories	Seeking for/tolerating	Avoiding the		
		the interaction with the	interaction with		
	•	S.	the S.		
	Seeking for/tolerating the	Consistently seeking	Relevantly		
Friendly	interaction with the S.	for/tolerating	alternating		
Approach		(N=13)	(N=15)		
episode	Avoiding the interaction	Irrelevantly alternating	Consistently		
	with the S.	$(\mathbf{N}=0)$	avoiding		
			$(\mathbf{N}=2)$		

Table 4.1.1.3. Number of dogs showing different response patterns in the Friendly- and Threatening approach episodes.

This table indicates that irrespective of whether the Threatening approach preceded or followed the Friendly approach, the majority of the dogs in both 'First-greeted' and 'First-threatened' groups showed either *Consistently seeking for/tolerating* behaviour towards the Stranger (7 and 6 individuals, respectively) or *Relevantly alternating* response (7 and 8 individuals, respectively) and there was only 1-1 dogs who showed *Consistently avoiding* behaviour. Interestingly, none of the dogs performed behaviour opposite of the behaviour of the Stranger (i.e. Avoiding in the Friendly approach and Seeking for/tolerating in the Threatening approach episodes), therefore none of them were categorized as *Irrelevantly alternating*.

The effect of gender on dogs' reaction to the Stranger

Since there are many examples in the literature suggesting that male dogs are more aggressive than females (e.g. Wright & Nesselrote 1987) and sex differences may also be significant in aggression towards human (e.g. Podberscek & Serpell 1997) we may assume that males and females react differently to the Stranger in our test situation as well. The analysis of the sex differences, however, showed no significant effect in Friendly approach episode (N(females)=N(males) = 15; U = 105, p = 0.77 for 'moving off', 'vocalization', 'attack' and 'contact seeking' and U = 112.5, p = 1 for 'avert gaze') nor in Threatening approach episode (U = 94.5, p = 0.46 for 'moving off', U = 104, p = 0.74 for 'vocalization', U = 112.5, p = 1 for 'attack', U = 102.5, p = 0.68 for 'avert gaze' and U = 106, p = 0.81 for 'contact seeking'). In accordance with this, we found that the two sexes were evenly distributed among the two main response categories (*Seeking for/tolerating* and *Avoiding*) in both episodes (p > 0.05 with Fisher's exact test).

In sum it seems that when approached by an unfamiliar human, dogs react in two different ways: half of them modified their reactions flexibly relying upon the changes in the human's behavioural cues while the others seemingly ignored these changes, and gave consistent (mostly friendly) response. Results suggest that in dogs this different responsivity cannot be attributed to sex. The question, however, that why some dogs showed consistent friendly behaviour while others tended to show sensitive and relevant change in their response to an unfamiliar human remained unanswered and called for further investigation.

Despite little experimental work many assume that there are breed-specific differences in their responsiveness to human cues. For example, analysing the behaviour of four breeds (Basenji, Shetland sheepdog, Fox terrier, Beagle) Freedman (1958) found that the manner of social interaction with humans had differential effect

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in a subsequent test (social inhibition of eating). Therefore a second experiment was designed to study whether dogs show breed specific differences in their reactions towards an unfamiliar person whose friendly behaviour cues are switched suddenly to threatening signals.

4.1.2. EXPERIMENT III/2

To test whether the breed can influence the reaction to friendly and threateningly approaching human we observed the behaviour of dogs from three breeds, which had originally different functions for the humans. The dog breeds are partially inbred, genetically isolated strains (Ostrander et al. 2000), and the gene flow is today restricted by breeders. Therefore, it seems reasonable to suppose that breed-specific differences have a genetic basis.

METHODS

Subjects

Sixty adult pet dogs (aged between 1 and 12 years) were involved in the present study. On the basis of their breed subjects were divided into three groups (N = 20 dogs in each). All groups were balanced for sex ratio (10 males, 10 females):

'Sled dog' group (mean age \pm SE = 3.6 \pm 1.6 years) consisted of huskies (6) and malamutes (14).

'Retriever' group (mean age \pm SE = 3.1 \pm 2.2 years) involved golden retrievers (12) and Labrador retrievers (8).

'Belgian shepherd' group (mean age \pm SE = 3.8 \pm 3.4 years) consisted of Tervuerens (9) and Groenendaels (11).

All breed groups represented the same age category (comparing mean ages: F(2,57) = 0.43, p > 0.05, ns).

Experimental procedures

The experimental arrangement and the exact procedure of the test was identical to that of described above in Experiment III/1 with the only exception, that all subjects are observed first in the Friendly approach episode, which was followed by the Threatening approach by the Stranger. Importantly, those dogs who showed any sign of avoidance or aggressive behaviours towards the friendly Stranger in the first episode were excluded from further analysis (three Belgian shepherds). The behaviour of the dogs was scored by using the same five variables (see Experiment III/1). Breed groups were compared with nonparametric methods (Kruskal Wallis tests with Dunn's post hoc tests). Mann—Whitney U test was used in order to compare the scores of the five behaviour variables between sexes.

RESULTS & DISCUSSION

Friendly approach episode

Dogs in all breed groups performed similar behaviour; 12 individuals of each group were scored as 'passive' and eight as 'friendly' when greeted by the Stranger.

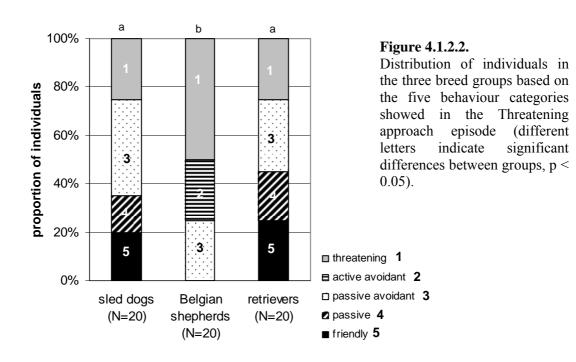
All breed groups were characterized by high 'contact seeking' scores (mean scores = 1.4 for all groups and no differences between groups were found: $chi^2 = 0$, p = 1).

Threatening approach episode

Comparisons of the five behaviour variables between breed-groups showed significant differences for 'moving off' ($chi^2 = 10.71$, p < 0.01), 'vocalization' ($chi^2 = 11.48$, p < 0.01) and 'contact seeking' ($chi^2 = 10.95$, p < 0.01) but not for 'avert gaze' ($chi^2 = 2.1$ p > 0.05) and 'attack' ($chi^2 = 3.49$, p > 0.05). Compared to sled dogs and retrievers, Belgian shepherds tended to move back towards their owners more frequently when the Stranger approached them threateningly (Dunn's multiple comparisons post-test: p < 0.05). Moreover, Belgian shepherds vocalized more often and for longer periods and obtained lower scores of 'contact seeking' towards the Stranger than retrievers or sled dogs (Dunn's multiple comparison post-tests: p < 0.05). Further, breed specific differences were found when dogs were classified into the five response-categories (Table 4.1.2.1, Figure 4.1.2.1).

		CATEGORIES								
		or/tolerating the ion with the S.	Avoiding ti	Avoiding the interaction with the S.						
Groups	passive	friendly	passive avoidant	active avoidant	threatening					
sled dogs	3 (0, 3)	4(2, 2)	8 (5, 3)	0	5 (3, 2)					
retrievers	4 (1, 3)	5 (2, 3)	6 (3, 3)	0	5 (4, 1)					
Belgian shepherds	0	0	5 (2, 3)	5 (3, 2)	10 (5, 5)					

Table 4.1.2.1 Number of individuals (females, males) showing different responsivity to the Stranger in the Threatening approach episode



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While a number of individuals responded 'passively' or 'friendly' to the threatening behaviour cues of the Stranger among sled dogs (7 out of 20) and retrievers (9 out of 20), none of the Belgian shepherds did. Instead, all of them avoided the interaction with the Stranger showing 'passive/active avoidance' (5-5 subjects) or 'threatening' behaviours (10 subjects). Comparing the distribution of the dogs' response in the three groups we found highly significant breed specific differences ($\sinh^2(2) = 11.42$, p < 0.01), that is retrievers and sled dogs were less likely to avoid the Stranger. Finally, in line with the results obtained in the first experiment dogs failed to show any sex related differences in their responsiveness in all three groups (p > 0.05 for all behaviour variables).

Although the interspecific form of aggression in dogs (i.e. aggression against humans) is often believed to be influenced by environmental factors such as socialization and individual experiences (Podberscek & Serpell 1997), the above results indicate the role of inherited traits leading to breed specific differences in the dogs' responsiveness to human. However, as we have no data about the consistency of the dogs' observed response, it is not clear whether or not the method used in the present study is a reliable procedure for tracing some of the personality characters (e.g. stress coping styles, aggression) in dogs. The purpose of the next experiment, therefore, was to make repeated behaviour observations on subjects from the same breed (Belgian Shepherds). Our analysis focused on the consistency of the dogs' behaviour shown towards the same stranger upon repeated tests.

4.1.3. EXPERIMENT III/3

METHODS

Subjects

Twenty-three Belgian Shepherd dogs and their owners were recruited on voluntary basis. (15 males, 8 females, mean age±SD: 5.2±0.7 years).

Experimental procedures

The experimental arrangement, the procedure of the test and the categorization of the dogs' response was identical to that of described above in Experiment III/2. However, after recording the first trial subjects were tested in the same situation 6-24 months later (the mean inter-trial interval was 12.8±1.0 months). Importantly, the location of the testing, the order of the episodes (i.e. Friendly approach, then Threatening approach) and the Stranger were the same as at the first occasion.

Data collection and analysis

Dogs showing the same type of responsiveness in the second trial as observed on the first occasion were given a score of one (labelling a consistent responsiveness) whilst those who changed from 'non-responsive' to 'responsive' or vice versa, and those who showed different behaviour towards the threateningly approaching stranger in the first vs. repeated trial were scored as 0 (labelling an inconsistent responsiveness). The consistency on the group level (regarding the responsiveness,

and the response category shown by the subjects) was analysed by binomial tests comparing the observed consistency to the chance level (0.5 in the case of two behavioural categories and 0.25 when analysing four categories). For the statistical tests the SPSS 10 statistical package was used.

RESULTS & DISCUSSION

Consistency of dogs' responsiveness: test - retest comparisons

Results show similar pattern when the repeated trial was conducted 6-24 months later. All dogs in the first episode (Friendly approach) of both trials showed Friendly/Passive behaviour towards the Stranger and majority of individuals (18 out of 23, 72.3 %) were scored as "responsive" in the first experimental trial. Interestingly, when the repeated trial was conducted 6-24 months later, dogs showed significant consistency in their responsiveness (p = 0.011). Subjects scored as "responsive" in the first trial showed a significant tendency to display the same type of reaction towards the Stranger during the repeated trial (p = 0.031), and all (p = 0.031) but one "non-responsive" dogs showed also consistent behaviour upon repetition. (However, it was impossible for the statistical analysis to yield p < 0.05 with so few subjects.)

Analyzing the consistency of different response categories

When responding to the Stranger in the Threatening approach episode dogs were assigned to one of the four categories (Friendly/Passive, Passive avoidant, Active avoidant, Threatening). Assuming that for an individual the probability value of exactly the same behaviour response is ½ we found a significant tendency to replicate the same behaviour towards the Stranger (binomial test, p=0.005; test proportion = 0.25). Importantly, however, when the dogs' willingness to replicate the behaviour performed in the first test was analysed separately in the 4 different response categories we found apparent differences (Table 4.1.3.1). Namely, whilst dogs showing either 'Threatening' or 'Friendly/Passive' behaviour in the second episode of the first trial towards the Stranger (N = 5 and 10, respectively) were disposed towards a consistent behaviour upon repeated trial (in 10 of 15 cases), there were hardly any dogs showing consistent behaviour in the Active or Passive avoidant categories (in 2 of 8 cases).

		2 nd test, Threatening approach					
		Friendly/	Passive	Active			
		Passive	avoidant	avoidant	Threatening	р	
1 st test,	Friendly /Passive	4	0	0	1	0.016	
Threatening	Passive avoidant	0	0	1	2	No stat	
approach	Active avoidant	1	0	2	2	0.555	
	Threatening	3	0	1	6	0.020	

Table 4.1.3.1. Cross-tabulation of the first and second test. The number of dogs performing different responses in the first and second trials is indicated. Cells indicating consistent behaviour are highlighted. The levels of significance (p) are highlighted where dogs showed significant consistency in replicating their response towards the Stranger. P values were calculated by binomial tests (test proportion = 0.25).

This apparent heterogeneity of the test-retest stability of the 4 behaviour categories suggest that different responses can be regarded as different manifestations of the same continuum representing the fear/aggression or approach/avoidance (Schneirla 1959) motivational conflicts. Accordingly, subjects showing a moderate (and/or ambivalent) behaviour (e.g. passive avoidance) towards the threatening human are ready to switch to a more definite response (active avoidance or threatening) upon repeated trials, whilst dogs performing an extreme of this continuum (threatening or friendly) are more consistent over time. Our analysis also points to the general problem, that the finer decomposition of the behaviour we apply, the less we can identify the observed variables with consistent "personality characteristics".

4.1.4. STUDY III. GENERAL DISCUSSION

The aim of Study III was to investigate the response of adult pet dogs to an unfamiliar woman (Stranger) who expressed social behaviour cues of friendliness and threat sequentially. The first experiment gave evidence that dogs (of various breeds) often show rapid changes of emotional and behavioural response in accordance with the flexible switching in the Stranger's attitude. The majority of dogs showed cues of tolerant, friendly behaviours upon 'Friendly approach' by the Stranger, but many of them gave various signs of avoidance or aggressiveness when the Stranger approached them threateningly.

We suppose that gazing cues of the Stranger played a key role in eliciting the dogs' response. Extended duration of gazing is often regarded as a form of ritualized aggression in wolves (Schenkel 1967) as well as in many social mammalian species. Many assume that human gazing function as a "social cue" for dogs as direct eyecontact is a typical component of the dominant displays (e.g. Line & Voith 1986, Serpell & Jagoe 1995). However, our results suggest that the approaching human's attempt to keep eye contact does not evoke unconditional fear or aggression, because in both ways of approaching (friendly and threatening) the continuous eye-contact between the dog and the human was aimed. Instead, it seems that not the gazing alone but other cues of human behaviour pattern, like body posture (straight vs. crouched), way of movement (continuous walking vs. halting) and verbal cues (friendly calling vs. speechless) have an influence on dogs' flexible response.

This interpretation is in agreement with some earlier observations which have suggested that dogs have a sophisticated ability for taking into account different aspects of human behaviour. For example, Millot (1994) found that dogs were able to discriminate between affiliative and agonistic body postures of children-like dummies, and provided evidence for the importance of gaze cues combined with signs of body posture, movement and olfactory signals in dog-human interaction (see also Lore & Eisenberg 1986).

Another important finding of Experiment III/1 is that dogs could be classified in two distinct categories. Half of the subjects proved to be "responsive" and they performed a flexible, relevant change in response to the altering cues of the Stranger (i.e. sought for contact when greeted friendly and avoided contact when approached threateningly). In contrast, the other half of the dogs can be regarded as "non-responsive" as they showed consistent (predominantly friendly, tolerant) response and seemingly ignored the changes in Stranger's behaviour.

This variability in the behaviour of dogs can be explained in different ways. First, differences in early social experiences may result in the observed differences in interaction with human (Fox & Stelzner 1966). However, we suppose that responsive/non-responsive dichotomy cannot be explained merely by major differences in our dogs' socialization prehistory or differences in their individual experiences with human. Our subjects represented a relatively homogeneous group from this respect: all dogs were kept as pets and they were recruited from dog training schools, where they regularly met unfamiliar dogs and people.

Second, it can be hypothesised that the two main response categories (i.e. relevant and flexible response to the Stranger or consistent friendly, tolerating reaction) may be attributed to breed specific differences. Similar effect was found by Svartberg (2006) indicating that selection for different purposes is associated with differences between personality traits (curiosity, sociability, aggressiveness) within many breeds.

The comparison of breed groups (sled dogs, shepherds and retrievers) has shown important differences and similarities among breeds. The relatively large number of "non-responsive" sled dogs and retrievers is in accordance with the widely accepted view, that sled dogs (malamutes and huskies) were originally working in cooperation with pack members and following the human leader's vocal instructions (and therefore a lower sensitivity to human behaviour is expected) while retrievers (Golden and Labrador retrievers) were bred for fetching the prey during hunt (so low aggression, low predatory motivation and readiness to retrieve could be advantageous). In contrast, all of the Belgian shepherds proved to be "responsive", and a significant proportion of them (50%) performed aggressive/threatening behaviour towards the threatening human. This is in line with the widely accepted notion that shepherd dogs had herding and watching functions and therefore a sensitive reaction to changes in others' behaviour and some degree of aggression against unfamiliar humans is expected.

In summary, we suggest that the flexible nature of dog behaviour is the result of an evolutionary process during which this species adapted to various degree of association with humans. The relatively long-term consistency of subjects' response (see Experiment III/3) further supports the view that this trait can be associated with personality characteristics in dogs and the 'Friendly/threatening Stranger' paradigm is a relevant experimental approach for studying the behavioural plasticity of dogs in general and the dogs' responsiveness to social releasers provided by human in more particular.

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4.2. STUDY IV. IMITATIVE ABILITY OF DOGS: REPRODUCING HUMAN ACTIONS AND ACTION SEQUENCES.*

Abstract

We present evidence that a dog (Philip, a 4-year-old Tervueren) was able to use different human actions as samples against which to match his own behaviour. First, Philip was trained to repeat nine human-demonstrated actions on command ('Do it!'). When his performance was markedly over chance in response to demonstration by one person, testing with untrained action sequences and other demonstrators showed some ability to generalise his understanding of copying. In a second study, we presented Philip with a sequence of human actions, again using the 'Do as I do' paradigm. All demonstrated actions had basically the same structure: the owner picked up a bottle from one of six places; transferred it to one of the five other places and then commanded the dog ('Do it!'). We found that Philip duplicated the entire sequence of moving a specific object from one particular place to another more often than expected by chance.

Although results point to significant limitations in his imitative abilities, it seems that the dog could have recognized the action sequence, on the basis of observation alone, in terms of the initial state, the means, and the goal. This suggests that dogs might acquire abilities by observation that enhance their success in complex sociobehavioural situations.

Topál J, Byrne R, Miklósi Á, Csányi V. (2006). Reproducing actions and action sequences: Do as I do in a dog. Animal Cognition 9(4): 355-368.

^{*}Based on:

INTRODUCTION

Increasing number of observations suggest that dogs show sophistication in situations where they acquire information from humans (for a review see Kubinyi et al. 2009). Recent results suggest that socially acquired information can be dominant over trial and error learning and that dogs might be in some sense predisposed to copy human behaviour. The importance of the social nature of demonstration in observational learning situations has been underlined by a study (Pongrácz et al. 2004), in which it was found that detour demonstrations around a V-shaped fence were ineffective when the human did not give any verbal attention-getting signals (even though the target object was visible in the hand) and did not make eye contact with the dog. Talking to the dog and shared attention, however, proved to be effective: dogs learnt to detour the fence after such demonstrations even when the human acted with empty hands. In another study Kubinyi et al. (2003) reported that dogs were influenced by the behaviour of their owners, even when the goal of the human behaviour was opaque. When dogs repeatedly witnessed aimless detouring behaviour of their owner, made after their usual daily walks, they gradually started to develop a similar habit, although the owner neither rewarded nor encouraged the dog's behaviour. Such an influence suggests that a capacity for action matching in the dog, and thus for learning by imitation, may have been overlooked.

Imitative processes have been defined as the acquisition of novel or otherwise improbable behavioural action in the observer as a result of observation of this action in another individual (Thorpe 1956), or as an animal learning some part of the form of the behaviour by observing other animal (Whiten & Ham 1992). In our investigation of the imitative abilities of the domestic dog, we focus on a fundamental feature—contingent behavioural similarity between the observed and the replicated behaviour.

The present study was designed to investigate whether a dog is able to show imitative behaviour, just in the sense of being able to use the behaviour of a human demonstrator as the basis for performing matching actions, either a single action or a sequence of actions. We used the so called 'Do as I do' paradigm (Hayes & Hayes 1952), which has been widely used for studying a subject's ability to imitate specified actions in great apes (Call 2001a; Custance et al. 1995; Myowa-Yamakoshi & Matsuzawa 1999), parrots (Moore 1993), and dolphins (Herman 2002). For success, a subject must perform matching behaviour in response to a variety of actions demonstrated by a human. The procedure involves training the subject to perform a small set of actions presented by the experimenter on verbal command (e.g. "Do it!"). After the subject reaches high levels of correct performance with the training set, they are tested with novel demonstrators and/or with novel (untrained) actions. Successful transfer to copying novel actions is taken as evidence that the subject has acquired the basic rule needed for imitative performance; that is, repeat an action after having observed it (Zentall 2001).

4.2.1. EXPERIMENT IV/1

In the first experiment, we limit our aims to provide evidence for recognizing of an imitation rule in a dog. The question was whether the dog would be able to choose a single, matching action from his repertoire in response to a variety of actions demonstrated by a human.

METHODS

Subject

The subject was a castrated male Belgian Tervueren, Philip, who was 4 years old at the beginning of the experiment. Philip was originally trained to assist his disabled owner by the trainers of a Hungarian charity (Dogs for Humans) for 6 months when he was 1.5 years old. Being an assistant dog, Philip was trained to open and shut doors, pick up items, fetch named items (e.g. mobile phone), switch on/off lights, pick selected items from supermarket shelves and put them in a basket, etc. Importantly, however, his training was based on traditional operant conditioning methods and "imitative techniques" (see below) were never used by the trainers. Subsequently, two members of our research team observed the dog over 3 years, in weekly 2-h visits, testing him on various sociocognitive and communicative tasks (e.g. Soproni et al. 2002). Apart from familiarisation to the various tasks, the researchers had never explicitly trained the dog at the start of the experiment. All visits were recorded on video.

Experimental procedures

We defined the match between the human's action and the trained action of the dog on the basis of functional correspondence (i.e. behaviours performed by the human/dog entail the same goal and—given the species-specific differences in the behaviour repertoire of humans and dogs—were executed in similar ways). For detailed description of the actions used in the "Do as I do" training, see Table 4.2.1.1. Importantly, all of the dog's actions had been previously trained by conventional methods (operant conditioning in the course of training for assistance work, or later by the disabled owner). However, these pairings of human demonstrations and expected dog responses were novel (i.e. dog was never taught to perform an action in response to human behaviour demonstrations) and somewhat arbitrary (i.e. pairings were arbitrarily predetermined from among possible alternatives). For instance, in response to human's jumps ("Jump in the air"), the dog was trained to jump in the air by raising only the two forelegs, while other possibility could have been rising on his hind legs (similarly to the standing human) and then jumping in the air.

Therefore, the task for the dog in this experiment was to recognize a human demonstration and to perform an action corresponding to it on the basis of the predetermined rule used in the training, i.e. functional correspondence, and the question of interest becomes whether the dog is in any way able to recognize and generalize this rule.

Training phase

Preliminary training

Three of the trained demonstration-action correspondences –'Turn around', 'Jump in the air' and 'Bow'– had already been partly trained by the owner using non-standardized methods. In our preliminary training, we refreshed Philip's knowledge of these pairings using conventional operant conditioning with the command 'Do it!', using access to a favourite toy to reward success. The rewarded action always matched the just-preceding action of the owner, which was always one of 'Turn around', 'Jump in the air' and 'Bow'.

Short name	Action as performed by the demonstrator (H)	The dog's (D) expected action for full correspondence
Turn around	H spins fast around the vertical body axis by pushing off using one leg	
Jump in the air	H jumps in the air by bending both legs at the knees	D jumps in the air by raising the two forelegs
Bow		D bows (play signal) by stretching both front legs forward and raising the hip
Lie down	H lies on the floor on the side of the body with partially retracted legs and arms	D lies on the floor on his belly
Put the bottle in the box	There are two plastic 0.5 l bottles on the floor next to a larger plastic container. H takes one of the bottles from the floor in right hand and places it into a container that is 30 cm away in front of the person	bottle from the floor in the mouth and places it into a container that is 30 cm
Take the bottle to the owner (O)	There are two plastic 0.5 l bottles on the floor next to a larger plastic container. H takes one of the bottles from the floor in right hand and takes it to the O who was sitting 3 m-s away	D takes the other plastic bottle from the floor in the mouth and takes it to the O
Move stick	There are two sticks placed horizontally on two chairs (2 m apart), H takes one stick and puts in on the floor	D takes the one remaining
Jump over	There are two sticks placed horizontally on two chairs, H jumps over them	There are two sticks placed horizontally on two chairs, Philip jumps over them
Give a bark	H gives a short 'bark'	D barks

Table 4.2.1.1. List and description of actions that were used by the trainer training and testing

"Do as I Do" training

During spring of 2002 (26 February to 30 April), Philip was trained by J.T. (Trainer) using operant conditioning, to perform on the command 'Do it!' one of an enlarged set of nine actions in response to functionally corresponding demonstration (in addition to 'Turn around', 'Jump in the air' and 'Bow', these were 'Lie down', 'Jump over' or 'Move a horizontally-placed stick', 'Put the bottle in the box', 'Take the bottle to the owner' and 'Give a bark', Table 4.4.1).

At the beginning of each training trial, the Trainer made the dog stand at the same place (using verbal commands and hand gestures known well by the dog), about 2 m away and facing the demonstrator and verbally attracted the dog's attention ("Philip, listen!"). This was followed by a demonstration of one of the nine

actions. After completing the action, the trainer took up his original standing position facing the dog and commanded the dog to perform the corresponding action ("Do it!"). If the dog remained passively in its standing position (i.e. did not act), then the command was repeated once at 5-s intervals, but no more than two repetitions were allowed. Philip received reward (a favourite toy) for some seconds only if he performed a correct response: the rewarded action always matched the just-preceding action of the trainer. Only the pre-trained three actions ('Turn around', 'Jump in the air' and 'Bow') were introduced in the first two sessions 1 and 2; then another three ('Put the bottle in the box', 'Lie down' and 'Jump over') were added in sessions 3 and 4; a further three ('Take the bottle to the owner', 'Move stick' and 'Give a bark') were added in sessions 5 and 6. Each of the nine actions was presented 17–28 times, giving 191 trials in total. The dog was trained regularly once a week in a session that lasted on average 15 min. The criterion of success was set as 80% correct responses of the total trials within a single session. Philip exceeded the criterion level in the 10th training session (when he reached 86% success). All trials were performed at the same location, and all objects used in any of the demonstrated actions were placed in the training area and were available for the dog before training commenced. This was done to ensure that the dog had the opportunity to do other actions in response to the demonstrated one if he chose to do so.

Testing phase

After 10 weekly training sessions, acquisition of the trained actions and generalization to untrained actions was tested formally, in the same context as in training (30 April to 1 June 2002). The subject's performance was both tested systematically by the Trainer (J.T.) and subsequently by a novel Demonstrator (A.M.) under identical conditions.

The Trainer performed all the nine actions only once in each session, for 10 sessions, resulting in 90 trials of the match-to-sample task which were video-recorded for later analysis. Actions were presented in a pseudo-random order previously determined by drawing lots and no reinforcement was given.

To control for the possibility of unconscious cueing of the human demonstrator, a novel Demonstrator then tested Philip under identical conditions. He was familiar to the dog but had never taught him before. Philip was tested on four of the trained actions ('Bow,' 'Turn around,' 'Lie down' and 'Jump in the air'), 14 trials with each action (56 trials in all, over 7 weekly sessions, each action was presented twice in each session). In this testing series, 'Control' trials were also included (1-3 trials in each session), in which no action was shown prior to the 'Do it!' command. In this case, the Demonstrator attracted the subject's attention ("Philip, listen!") and looked over the head of the dog for 2–3 s. Then the command ("Do it!") was given, and the demonstrator waited 5 s for the subject's reaction.

Over the same time period, we tested Philip's response to demonstrations that had never been shown in the course of training (see Table 4.2.1.2). Untrained actions were demonstrated by either the Owner (7 cases) or the Trainer (9 cases). Actions were chosen to differ from each other on the basis of type of action (body-oriented, manipulative, environment–oriented) and complexity (number and length of action sequences). In any one session, no more than three simple actions or complex action sequences (in total 16 – see Table 4.2.1.2.) were shown to Philip and followed by the "Do it!" command. All demonstrations were shown to the dog only once. Importantly, all of the "untrained actions" consisted of behaviour element that are

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already part of the dog's repertoire (being an assistant dog, Philip was able to open doors, fetch objects, etc.). Therefore, these demonstrations were novel to the effect that the dog never met such action sequences in the 'Do as I do' tasks before.

Short name (type of action):		Action level descrip	otion	
M= manipulative; B= bodily/motor	Human (H) demonstration	Dogs' (D) expected response	False action	Correspon- dence scores
Move shoe (M)	H bends body & picks up one of the two shoes by hand from the floor, moves shoe to the predetermined point, releases shoe	D picks up the other shoe from the floor by mouth(1), goes to the same point(2), releases shoe(3)		6
Throw bottle (M)	H bends body & takes bottle in right hand, throws bottle to other person	D takes bottle in mouth(1), goes to other person(2), gives bottle to him(3)		6
Go round human (B)	H goes to other person, goes around him, goes back to starting place	D goes to other person(1), goes around him(3), goes back to starting place(4)	Turns around with bent backbone, orienting his head toward his tail(2)	4
Pull arm (B)	H goes to other person, pulls his arm vividly by hand, goes back to starting place	D goes to other person(1), pulls his arm vividly by mouth, goes back to starting place(4)	Bows by stretching both front legs forward and raising the hip(2) snuffles at human's right hand(3)	3
Open/close door	H goes to door, opens door by hand (using the door-handle), closes door,	D goes to door(1), opens door by mouth (using the door handle) (2), closes door(3),		6
	H crouches down, performs scratching movements in the sand by both hands, stands up	D bows(1), performs scratching movements in the sand(3), stands up	Jumps in the air by raising the two forelegs(2)	3

Table 4.2.1.2. Schematic description of Philip's responses (based on the agreements of the different observers) and his correspondence scores in the demonstrations of the 16 untrained actions (**continued on the next page**)

Short name (type of action):		Action level description							
M= manipulative; B= bodily/motor)	Human (H) demonstration	Dogs' (D) expected response	False action	Correspondence scores					
Take out put in object (M)	H opens cupboard door by hand, takes out object, puts object into the bin	D opens cupboard door by mouth(1), picks up and takes out object (by mouth)(2), puts object into the bin(3)		6					
Go in/come back (B)	H goes through open door into other room, turns around, comes back	D goes through open door into other room(1), turns around(2), comes back		4					
Pull cloth (M)	H goes to shelf, picks up the cloth by hand, pulls the cloth and releases it	D goes to shelf(1), picks up the cloth & pulls it by mouth(2) releases the cloth(4)	Goes to the owner with the cloth in his mouth(3)	5					
Push swing (M)	H goes to swing, pushes swing by hand, goes back to starting place	D goes to swing(1), pushes swing by nose(2), goes back to starting place		4					
Lying down on top of the cupboard (B)	H goes to cupboard (70 cm high), crawls on top, goes back to starting place	D goes to cupboard (50 cm high)(1), crawls on top, goes back to starting place	Lies on the floor on his belly(2)	2					
Crawling into the cupboard (B)	H goes to cupboard, crawls into cupboard, comes back	D goes to cupboard(1), crawls into cupboard, comes back(2)	Goes to cupboard again and look in3	2					
Put the tape on the chair (M)	H bends his body & picks up one of the two tapes from the floor by hand, moves tape to chair, releases tape	D picks up the other tape from the floor by mouth(2), moves tape to chair(3), releases tape(4)	Puts his left paw on the humans leg(1)	3					
Go and turn (B)	H goes to the far end of the room (3 m), turns around (1.5 turns), comes back	H goes to the far end of the room -3m (1), turns around -1.5 turns, comes back(2)		3					

Table 4.2.1.2. continuation. Schematic description of Philip's responses (based on the agreements of the different observers) and his correspondence scores in the demonstrations of the 16 untrained actions (**continued on the next page**)

Drinking (B)	H goes to bowl on his hands and knees, laps from bowl, comes back	laps from bowl(2),		4
Push child toy (M)	H bends his body, pushes the toy forward by hand	D bows(1), pushes the toy forward by nose		2
	63/94			

Table 4.2.1.2. Schematic description of Philip's responses (based on the agreements of the different observers) and his correspondence scores in the demonstrations of the 16 untrained actions. Action-level descriptions of the demonstrations and 'perfect' responses are given, with schematic data on Philip's actual response. Due to species specific differences between motor and manipulative abilities in dogs and humans, each action of the dog that are not identical but functionally homologue to human demonstration were regarded as correspondent response (e.g. while human uses his hand; dog picks up things by mouth). Numbers in parentheses indicate the order of presentation by Philip.

Data collection and analysis

Two independent observers watched videotapes of each test trial for trained actions, and recorded whether the dog's response corresponded with the demonstration or not. They were given detailed descriptions of the nine actions demonstrated by the trainer (see Table 4.4.1.); however, they watched just the dog's action and could not see what the human demonstration was. Inter-observer reliability was found to be high (percentage agreement: 99%, Cohen's kappa coefficient: 0.95). We assumed that chance performance would be success on 1/9 trials because altogether nine different match-to-sample pairs were demonstrated. Note that this is rather conservative, given the fact that theoretically the subject had the possibility to perform any other action at all, rather than just those trained in that situation.

For the analysis of the untrained actions (Table 4.2.1.2) similarity between the demonstrated action and the dog's behaviour was assessed by parallel coding of the recordings by two trained observers. They were asked to take account of two variables in measuring similarity: 'Content', i.e. whether a particular behaviour performed was part of the demonstrated sequence, and 'Sequential correspondence', i.e. whether it was enacted at the appropriate place of the action sequence. For example, a score of 2 was given if the first action in demonstration (labelled as 'A') was the first element of the subject's response, whereas a score of 1 was given if action "A" was performed by the subject as the second or third element of his response; that is, if the action was displayed but not at the corresponding place in the sequence. Scores were summed for each action. All but one demonstration of untrained actions contains a sequence of three actions (one consisted of only two) so the maximum 'Correspondence score' for a demonstration of a three-action sequence could be 6 (and 4, respectively). Inter-observer reliability scores were measured between the two observers for the dog's performance. Percentage agreements and Cohen's kappa coefficients were calculated for both 'content' (91% and 0.75 respectively) and 'sequential correspondence' (85% and 0.57 respectively).

We should note that the scores for correspondence given by the two trained observers might have been biased because they knew each time which one of the demonstrations had been shown to Philip, and therefore they were looking for some resemblance between what the dog did and what they knew it had been shown. In order to guard against this possibility, we also used a blind observer. Video recordings about the behaviour of the dog in the 16 demonstrations of untrained actions were shown to this observer, who did not know each time what action or sequence of actions had been shown to the dog, and he was asked to describe what the dog had done. The occurrence and sequence of actions identified by the blind observer was compared to that of given by one of the trained observers and similar levels of reliability were found compared to the case of the two trained observers (87% and 0.66 for the contential agreement; 82.5% and 0.54 for the sequence of the observed actions).

This latter analysis suggests that the poor inter-rater reliability scores for untrained actions (especially in the case of sequential correspondence) allow only limited interpretation of the results. Therefore, in order to avoid overestimation of Philip's performance in case of any kind of disagreement between the raters, the dog's action was considered as "mismatching" for the analysis.

RESULTS

Test trials with the trainer

Overall performance in response to human demonstrations was markedly above chance (one-sample Wilcoxon signed-rank test $T_-=0$, p=0.007). Philip showed "mismatched" behaviour on 27.8% of the total trials and all of those could be either categorised as another of the nine trained actions (16.7%) or as "no response" (11.1% of the total trials); we did not observe other types of action at all (Table 4.2.1.3).

Analysing the nine actions separately, Philip showed no significant variation in level of correspondence across the actions demonstrated by the trainer (Friedman ANOVA, ${\rm chi}^2=10.7,~p=NS$), and performed significantly better than chance in all cases (binomial tests, p < 0.001 for all actions except for 'Bow', where p < 0.01 was found). We also examined whether there was a difference between "manipulative" ('Put the bottle in the box', 'Take the bottle to the owner' and 'Move stick') and "body-oriented" actions (the remaining six). Philip showed similar performance in response to these two types of actions (correct responses: 22/30–73.3% and 43/60 – 71.7%, respectively).

Test trials with a novel demonstrator

Philip's response matched the behaviour of the novel demonstrator significantly above chance (one-sample Wilcoxon signed-rank test, $T_+ = 5$, p = 0.041) and this level was similar to that observed in the trials with the Trainer (68.6% versus 72.2%; Table 4.2.1.4).

Comparing Philip's performance in the four different tasks, we found that he showed more "mismatched" behaviour when 'Bow' was demonstrated than when 'Jump in the air' (Friedman ANOVA, $chi^2 = 15.3$, p = 0.0016; Dunn's post hoc comparisons: 'Bow' vs. 'Jump in the air' p < 0.05) was shown. However, the dog performed significantly better than chance in all cases (binomial tests, p < 0.01 for all action except for 'Bow', where p < 0.05 was found).

Importantly, Philip showed no sign of "guessing" the desired in the 'Control' trials. Instead, he gave a response corresponding to the behaviour performed by the novel human demonstrator in these as in other trials: i.e. in 92.8% of control trials,

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Philip performed no action in response to the command "Do it!" given by the (passive) demonstrator.

	Actions performed by the dog										
	Turn around	Jump in the air	Bow	down	Put the bottle in	Take the bottle to owner	Move stick	Jump over	Give a bark	Other	Correct (%)
H. demo.											
Turn around	6	1								3	60
Jump in the air		7								3	70
Bow		2	5	2						1	50
Lie down				6	1	2				1	60
Put the bottle in					6	4					60
Take the bottle to owner					1	9					90
Move stick				1			7			2	70
Jump over								10			100
Give a bark	1								9		90
Total							72.2				

Table 4.2.1.3. Actions performed by the dog (Philip) in response to different human demonstrations (H. demo.)

		Actions performed by the dog						
	Passive Bow Turn Lie Jump in the air				Correct (%)			
Actions demonstrated by novel Demonstrator								
Control (no demonstration)	13	1				92.8		
Bow	2	6		5	1	42.8		
Turn around	2	1	8	1	2	57.1		
Lie down	2	2	1	8	1	57.1		
Jump in the air		1			13	92.8		
Total						68.6		

Table 4.2.1.4. Philip's performance to demonstrations by the novel Demonstrator (A.M.)

Test trials with untrained actions

Matching performance in response to these demonstrations was found 67% (63 out of a total possible 94 in the correspondence score, see Table 4.4.2., and the Methods section for details of calculating scores). This is comparable to the dog's performance in test trials with trained actions. The demonstrations of the 16 untrained actions contained 47 separate elements (15 demonstrations with 3 actions, and 1 with 2 actions). According to the agreed decisions of the observers, corresponding behaviours were observed to most of the demonstrated actions (36/47; 76.6%) and the majority of them (27/47; 57.4%) were performed by the dog in the same sequence as it was demonstrated. It is worth noting that the probability of this level of agreement by chance, on the null hypothesis of random performance, is very low.

We also categorized the demonstrations as "manipulative" (8 cases – see the descriptions in Table 4.4.2.) or "bodily/motor" (the remaining 8) and found that Philip performed at a marginally lower level of correspondence in response to "bodily/motor" actions than 'manipulative' ones $(T_- = 90, p = 0.090, which approaches significance).$

DISCUSSION

Superficially, dogs do not seem ideal subjects for this experimental approach. In contrast to children and great apes, dogs have a very different body schema to that of humans. Nevertheless, we found clear suggestions of the presence of some imitative ability in the performance of the tervueren Philip. After a relatively short period of 'Do as I do' training, Philip was able to successfully choose the correctly matching action from his own repertoire, in response to a variety of actions demonstrated by a human. The dog was not only able to use the behaviour of a human demonstrator as a sample, against which to match his choice of a corresponding action, but seemed to grasp the idea of matching-to-sample in relatively short time. He showed transfer both to a new person to be observed, and new actions to be matched.

Test trials with the 'Novel demonstrator' shed light on the dog's ability to generalize while performing 'Do as I do' task. Although some stimulus generalization is expected even in associative learning, depending on what features of cue stimuli the subject actually discriminates/attends to, the dog's behaviour here suggest a flexible application of the "do same" rule. This was confirmed by his response to test trials with untrained actions. Philip transferred without explicit training to actions in his pre-existing repertoire that had never been used in the do-as-I-do paradigm before. Evidently, he understood the task as one of finding a functional match in his behaviour to the human behaviour demonstrated. Note, however, that Philip was not required to perform a wholly new routine in any of the 16 untrained action-demonstrations: all that was required for a correct response was selection on the basis of behavioural correspondence.

Although the present study with Philip is only partly comparable to other "do as I do" studies (because in our case "untrained actions" were not really novel), some aspects of Philip's imitative performance within his physical/motor limits has shown similarities to that of found in great apes (Call 2001a; Custance et al. 1995; Myowa-Yamakoshi & Matsuzawa 1999), parrots (Moore 1993) and dolphins (Herman 2002). Since we have observed this ability only in one dog, our conclusions cannot

immediately be assumed true of dogs in general; however recent studies (Miller et al. 2009, Huber et al. 2009) have successfully replicated these results providing further support for dogs' imitative abilities.

Philip's ability to recognize behavioural correspondence between his own and a human's actions extends beyond more-or-less exact correspondence (e.g. mouth licking) to cases of merely functional correspondence (e.g. human takes object in hand; dog picks up object in mouth). This feature of our data, a consequence of the obvious species-specific differences in the demonstrator's and the dog's manipulative capacities, fortuitously allows us to see that Philip's ability to generalize behaviour operates at a non-superficial level. However, dogs, like parrots, have a restricted motor ability to act on themselves (body-oriented actions) or on the environment, in comparison to apes, which may mean that they have correspondingly less sophisticated abilities to mentally represent such actions.

4.2.2. EXPERIMENT IV/2.

Although some elements of the demonstrations in Experiment IV/1 had a sequential character, there was no specific attempt to test the dog's understanding of the sequential nature of real behaviour. In the second experiment, therefore, we aimed specifically to test the dog's ability to match a sequence of human actions, on the basis of observation. In the course of a 9-week period, a tester repeatedly demonstrated the same action sequence to Philip (transferring an object from location A to B), each time with different constituents, commanding the dog to do the same action ("Do it!"). Importantly, in this experiment, Philip received no training and none of his actions was rewarded or punished discriminatively.

Our question was whether the dog would show a spontaneous preference for repeating the particular sequence of actions of the human partner. We begin from the argument that, in order to understand everyday means—ends relationships and the intended outcomes of actions by human partners, the dog may possess some way of encoding the different relationships that exist between those behavioural actions and objects in the world (Byrne & Russon 1998). For instance, suppose a dog observes a human take an object and put it in a box. Although the actions themselves may be familiar ones in the dog's repertoire, in order to understand the human's behaviour sufficiently to copy it, the dog needs to distinguish the roles of agent, object and result of the observed action. Thus, the task of copying a sequence of human actions can be seen as a measure of the dog's understanding: in particular, if Philip's behaviour correctly matches the semantic roles of the objects and actions, then it suggests the possibility that he has at least some rudimentary understanding of some "semantic relationships" that hold among the constituents of the action (Byrne et al. 2004).

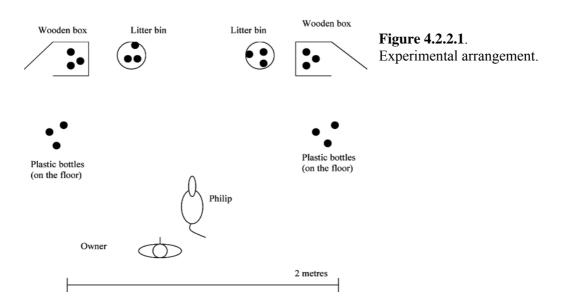
METHODS

Experimental procedures

Testing was carried out over a 2-month period, in a large room in the owner's flat. During the 2 years break since Experiment IV/1, the dog had had regular opportunity to practice the 'Do as I do' task with the original nine trained actions and

with demonstrations given by both the Owner and the Trainer. Neither of them had used the "Do it!" command in other situations.

Two identical litter bins and two identical open wooden boxes were placed in line on the floor (Figure 4.2.2.1). The cover of each litter bin could be opened by pressing a lever on the bin; the wooden boxes were open and lay on one side, turned away from the dog. Both bins and boxes originally contained three identical plastic bottles, and there were also three plastic bottles at predetermined points on the floor on both sides of the owner and the dog. This layout allowed for six potential target locations to which bottles could be carried or taken, with three plastic bottles already in each.



All commands were given by Philip's owner, following a precise protocol. Before each trial, the owner made the dog sit at the same, predetermined place, so that the owner stood about 2 m away from the line of the boxes and bins, while the dog's nose to the box/bin line was 1.25-1.75 m. The dog faced toward the targets and was thus not in visual contact with the owner who was positioned behind the dog. He then verbally attracted the dog's attention ("Philip, listen!"), and then gave the demonstration. All demonstrated actions had basically the same structure: the owner picked up a bottle from one of the six places and transferred it to one of the five other places; thus, there were $6 \times 5 = 30$ different possible sequences. After completing the action, the owner took up his original position (behind the dog) and commanded the dog to perform the corresponding action ("Do it!"). The command was repeated once in every 5 s until the dog transferred one of the bottles (in most cases Philip responded after the first command and there were no trials on which he did not respond after three commands). The trial was considered complete if the dog released the bottle at any place in the room. After each trial (regardless of the dog's performance), Philip was praised verbally and petted by his owner. As human's transferring the bottle may result in a "trail of odour," which marks the route between the start and goal location, we needed to eliminate the discriminative effect of human odour cues. Therefore, before each trial, when the owner placed the 18 plastic bottles in the 6 potential target places without the dog being present, he fingered all the bottles and passed all possible routes.

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The owner demonstrated each of the 30 possible sequences once, in a randomised order, and repeated the same procedure after a 2-week break. The first set of trials took 3 weeks to complete (10 trials per week, not more than 2 trials per day). The second set of trials took 4 weeks to complete (6, 10, 10 and 4 trials per week, less than 3 trials daily).

Note that the litter bin had to be opened by pressing the lever in order to put in or take out an object, whereas no action was needed in the case of the wooden box. As a fully trained assistance dog for his disabled owner, Philip was already used to tasks of this structure in his work; and, moreover, he was familiar with the basic behaviour patterns that made up the sequence, such as going to a box or litter bin, taking out an object and dropping it somewhere else. Thus, the key variables to which the dog needed to pay attention in order to copy the transfer sequence were just the location of start and finish.

Data collection and analysis

We classified the locations of the objects into five categories: 'Start', where the owner had picked up a bottle; 'Goal,' where the owner had put the bottle; the symmetrical places to each of these, which we termed 'Start-twin' and 'Goal-twin'; and the two other locations in the experimental arena, lumped as 'other'. In order to analyse the dog's success in copying the sequence, assuming that he does indeed copy the basic structure of the action, we note that there are six places from where he could pick up a bottle, and there are also the same six places where Philip could drop the bottle ($6\times6=36$ possible responses). Accordingly, the chance performance was calculated as 1/36 for the action involving bottle transfer from 'Start' to 'Goal' sequence and the observed frequencies of different action-sequences were compared to chance frequency by binomial tests.

RESULTS

In every trial, Philip was successfully induced to copy the basic structure of the demonstrated action: that is, he took a bottle from one place to another, without discriminative reward. Philip tended to pick up the bottle from and take it to the same places as had the human demonstrator significantly more often than expected by chance ("same start" 28 cases out of 60 trials, binomial test, test proportion = 0.167, p < 0.0001; "same goal" 21 cases out of 60 trials, binomial test, test proportion = 0.167, p < 0.0001).

Analysing the whole sequence of the dog's actions shows that Philip executed the exact same sequence of bottle-transferring actions as demonstrated by the owner in 16/60 trials (Table 4.2.2.2.), which is again markedly more frequent than expected by chance (binomial test, test proportion = 0.028, p < 0.0001). Moreover, some of Philip's errors were close to the correct response. For instance, when the bottle was picked up at the correct start but dropped off at the goal-twin location, the confusion amounts to merely a left/right confusion of goal location. This "erroneous" response was observed significantly more frequently than expected by chance (6/60 trials, test proportion = 0.028, p = 0.001). Interestingly, we also observed a precisely reversed sequence of the demonstrated actions more frequently than expected by chance (7/60 trials, test proportion = 0.028, p = 0.02); in these cases, Philip picked up a bottle at the goal location and moved it to the start location.

Place where the bottle is			dropped off					
	Start	Goal	Start-twin	Goal-twin	Other			
picked up								
Start	0	16 ***	0	6 **	6			
Start-twin	0	1	0	0	2			
Goal	7 **	2	2	3	1			
Goal-twin	2	0	0	0	2			
Other	2	2	0	2	4			

Table 4.2.2.2.

Number of Philip's different actions as response to the demonstrations (picking a bottle from start location and transferring it to the goal location)

Difference from chance level:

** p=0.001

** p=0.001, *** p<0.001.

Finally, we should consider the possibility that Philip was being shaped by unconscious cueing (given by the owner) and the dog's performance mirrors a Clever Hans effect. Assuming that Philip has a sophisticated behaviour-reading ability regarding his owner and in the test situation his response was 'governed' by the subtle behaviour cues of the owner, we should expect a gradual improvement in his bottle-transferring accuracy over the course of the trials. However, comparing the results in the first and last 10 trials (trials 1-10 vs. trials 50-60.) we did not find significant differences (N1 = N2 = 10, U = 50, p = 1), suggesting that Philip did not learn to utilize unconscious cueing as testing proceeded.

DISCUSSION

The dog was able to organise his behaviour on the basis of the human actions, translating not only the basic type of familiar action (carrying an object from place to place) from the observed demonstration to his own behaviour but also copying the details of start and finish locations more frequently than chance performance.

Although individuals can manipulate and use relational phenomena without understanding the cause–effect relationships involved (see e.g., tool-using in capuchins; Visalberghi 1993), our results raise the possibility that the dog had some understanding of the action sequence in terms of the initial state, the means and the goal. Seeing the demonstration, he not only carried out "place to place carrying" but tended to match the specific location at which the object was picked up, and that at which it was dropped. Like many humans, he showed a distinct tendency to make left/right confusions, and if he were "given the benefit of the doubt" on the occasions when he carried the object from the correct starting place to the mirror image of the correct finish (an improbable error, by chance), his copying of the sequence after only a single demonstration reaches 37%. However, he did also confuse the start and finish locations, though such errors occurred at a lower frequency (12%).

It may be helpful to view the dog's performance in terms of a theory developed to describe sentences in linguistics, case grammar (Byrne et al. 2004; Fillmore 1968). In case of grammar, each verb (action) structures a set of semantic cases; for example, the verb "carry" has cases for agent (the animate actor), object (the object or material moved), and optionally two locations, from and to (places from which and to which the object is taken). Although developed for natural language, case grammar terms can also be used to interpret animal behaviour. A

wolf's behaviour in carrying food for its puppies, for instance, may be represented in terms of the "carry" case frame with agent (wolf), object (meat), to-location (den) specified. Structuring in terms of a framework of cases can also be used to decode the action of others. If an animal is able to decode another's behaviour in this way, then their understanding of the other individual's behaviour would be a matter of first recognising the action, and then "filling in the slots" in the case frame, for each of the semantic categories it specifies. We find this account helpful in understanding Philip's achievements in our experiments. A dog can be said to understand the meaning of carrying in some sense if it has the ability to perform the action, and since carrying is a part of the ethogram of the wolf, it is to be expected that all dogs have this ability. Transferring items from one place to another may be part of the species-specific repertoire of dogs; certainly, there was no doubt that Philip possessed this action routine in his repertoire before our experiment. However, carrying cannot be regarded as a simple movement pattern, but a structured framework with "cases" or "slots" for agent, object, and to-and from-locations. Thus, when a dog observes a human demonstrator carrying an object, it may be said to "understand" what the other is doing if its representation includes the specific contents of each slot.

At the time of this experiment Philip had already been trained to 'do as I do,' i.e. substituting himself for the human as agent of an observed action, so he was without further training able to copy (to a certain extent) the entire sequence of moving a specific object from one particular place to another. In contrast, "to put an object1 on object2" is not part of the species-specific repertoire of dogs, so without learning this action individually, a dog cannot be expected to understand the meaning of this action without specific training. Experiment IV.1 showed that, given such training, Philip was able to augment his repertoire accordingly to some degree, and indeed his training as a helper for a disabled human focuses on developing an appropriate, human-relevant repertoire. We suggest that such experience plays a substantial role either in enhancing imitative performance or in generating imitative ability.

4.2.3. STUDY IV. GENERAL DISCUSSION

Extensive testing of Philip clearly demonstrated that he was able to recognize similarity between the observed and the replicated behaviour and use the behavioural actions of a human demonstrator as cues for corresponding actions. It seems that dogs have some imitative abilities, and they are able to map observed behaviour of the human demonstrator onto the corresponding motor scheme of the self. Although data show fair performance in copying actions and action sequences, the possibilities of lower level underlying mechanisms (goal emulation and simple local enhancement) cannot be completely dismissed. While dolphins and great apes often regarded as imitative generalists (Herman 2002; Nielsen et al. 2005), based on these findings, Philip's imitation more closely resembles the narrower pattern characteristic of task specialists – with limited "case grammars".

Being a specially trained service dog, someone may assume that Philip's performance was based on a species-typical "transport item" routine. It seems that he succeeded well on transporting items to/from target locations (relevant task for an assistant dog and biologically relevant task for the species) and in some cases had more difficulty combining other actions with the transport-item routine (e.g.

spin/turn around at the target location, climb into/onto target location, etc.). This suggests the importance of working experience and species-specific skills (fetching objects) in the dogs' imitative performance and points to the role of associative processes in mastering 'Do as I do' tasks. However, imitative processes in bird species (Zentall 2004, 2006) and the results of our dog here raise the question whether associative learning is sufficient to yield a capacity for such social learning or, alternatively, more sophisticated cognitive processes are necessary to understand the phenomena. This question is underlined by the present study pointing to the potential role of relational understanding in matching functional action sequences.

Results suggest that our subject may be able to detect and reproduce some semantic relationships among actions objects and places. Note that our view of imitative behaviour in the dog as a matter of mapping novel entities into pre-existing case slots may help explain some of the superior abilities of "enculturated" subjects in imitating some actions demonstrated by humans (Call & Tomasello 1996; Tomasello, Savage-Rumbaugh & Kruger 1993), since these animals will have an augmented repertoire of actions with which to understand human actions. Since our subject already knew all test entities, Philip's behaviour in the 'Do as I do' tasks could be explained by the insertion of some known entities into case slots. Some of the test entities may have been novel relative to a particular routine (i.e., twirling at a target location vs. picking something up), but Philip's extensive training history reduces the range of known entities that were possibly novel to specific routines. Concerning novelty, note that although Philip did not learn anything new in terms of his motor patterns, he was able to make clear distinction between different forms of human behaviour and learn to use these as samples, against which to match his own, corresponding behaviours, on the basis of resemblance to the demonstrated action. This ability has sometimes been described as imitation (e.g. Heyes & Sagerson, 2002); however, scholars have traditionally reserved "imitation", or "imitationlearning" or "observational learning" for cases where a novel performance is acquired, at least in part, by observation (e.g. Byrne & Russon 1998). By traditional criteria, Philip's performance at copying single actions did not show imitation, and we suggest "response facilitation" (Byrne 1994) is a clearer description, since the observed performance might have been caused by "priming" or "triggering" of some pre-existing behaviour of the dog. Although mirror neurons (Rizzolatti et al. 1996) have not so far been detected in dogs, several researchers have noted that a mirror neuron system is a highly plausible mechanism for response facilitation (e.g. Bates & Byrne 2010; Rizzolatti et al. 2002). Philip's partial success in copying a structured sequence of action (Experiment IV/2) may go beyond response facilitation, since he showed a significant tendency to keep distinct the semantic roles of the action, in particular, the potentially confusing pair of to-location and from location.

Although Philip failed to show any compelling evidence of action-level imitation, the interpretation of his copying behaviour in terms of "case grammar" is in some ways akin to programme-level imitation (Byrne & Russon 1998). Given the limited experimental data, however, the plausibility of case grammar hypothesis and its relevance to programme/action level imitation are unclear at present.

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4.3. STUDY V. WILLINGNESS TO FOLLOW SOCIAL RULES - A COMPARATIVE STUDY ON DOGS AND HUMANS.*

Abstract

Using a traditional object permanence paradigm here we investigated adult pet dogs' and children's ability to identify and use social rules that are formed by the interaction with the experimenter during the consecutive object hiding and search tasks.

Experiment V/1 was designed to demonstrate that such social rules may have an independent influence on the performance of both children and dog subjects. The behaviours of preschool humans and adult pet dogs were compared in a modified version of the successive invisible displacements task ('No object' condition) and in a similar task in which, however, the location of the target object was well known by the subjects ('Game' condition).

During the 'No object' condition most of the children and dogs performed a full and systematic search of all potential hiding places. However, results in 'Game' condition indicate that piagetian object permanence tests may be interpreted by both dogs and humans not only as object hiding and finding tasks, but, alternatively, as social-behavioural games of different sorts that may contribute to the systematic search performance.

A second experiment was directly designed to demonstrate the influential effect of social rules on dogs' behaviour in the object hiding and finding tasks. Results show that the functional opacity of the Hider's behaviour (i.e., performing both functionally relevant and irrelevant actions upon hiding) enhanced the emergence of "obeying social rules" (i.e., dogs tended to perform search behaviour, although they knew the location of the target object). We suggest that during their domestication dogs may have been selected for certain human-like capacities such as recognising and following social rules in the context of interacting with humans.

Topál J, Kubinyi E, Gácsi M, Miklósi Á. (2005). Obeying social rules: A comparative study on dogs and humans. Journal of Cultural and Evolutionary Psychology 3(3-4): 213-238.

^{*}Based on:

INTRODUCTION

In humans rule-following behaviour is one of the mechanisms for synchronisation of group behaviour and at the simplest level it can be considered as a behavioural tool for minimising conflicts. There is a hierarchy of rules from very simple behavioural rules to more complex cultural rules in our species, and various forms of rules are tied to our linguistic communication system, i.e. they can be formalised in language. Following a rule is closely connected to the rank order of the group. Forming and keeping a rank-order is transformed to a new organizational level by obeying a depersonalized dominance. The dominant individual is substituted by a socially accepted rule (Csányi 2000). De Waal (1996) suggested that the context of rule learning is either agonistic, when obeying the rules minimize the negative consequences in social interactions or collaborative (play, cooperation, communication) which leads to maintaining the social interaction.

The social rule is a mental construction which can be formed by the observation of the behaviour of others and this mental-constructional skill might be an important factor for the development of moral systems (Flack & de Waal 2000).

In non-human animals, however, the term "social rule" has a different meaning. Social rules can be mastered by two means:

- (i) Prescriptive rules are upheld by reward and punishment as it was shown for instance, in the cases where dominant-submissive interactions are controlled by social rules (see e.g. "respect of possession" studies on macaques Kummer & Cords 1991; and on baboons Sigg & Falett 1985). These rules are in most cases enforced, and they do not apply equally to all members to the community (i.e. they are not reciprocal).
- (ii) Descriptive rules, however, are formed without an exterior constraint, such as when females defend their offspring from the conspecifics in aggressive situations (de Waal 1991b). Descriptive rules describe a typical response to a specific social situation, while the statistical regularities of prescriptive rules are perceived, complied with and/or enforced by the individuals (Flack et al. 2005). In highly social species following social rules could lead to a more flexible and complex grouphunting, sharing resources and picking up behavioural traditions.

There are three main factors in nonhuman social species that are supposed to have an enhancing effect on the emergence of social rules: (i) flexible motor patterns (trainability), (ii) dependence on social mimesis, (iii) ability of role reversal (e.g. in play or in cooperation) and (iv) acceptance of division of resources (e.g. food sharing). In line with this approach, de Waal (1996) suggested that dogs are an ideal subject for social rule investigations. "Canids have an excellent sense of social rules, which allows for order within the hunting pack and explains their trainability for human purposes..." (p. 94.) Moreover it is increasingly assumed that the social cognitive capacities of dogs, including their propensity for recognising and following social rules in the context of interacting with humans, have been formed by the cognitively challenging complex human social environment (e.g. Cooper et al. 2003; Miklósi 2007).

It has been reported, for instance, that dogs can adopt spontaneously a novel, arbitrary (actually pointless) behaviour as a result of interaction with their owner (Kubinyi et al. 2003). Namely when dogs could witness a causeless detouring behaviour of their owner after their usual daily walks, they gradually started to develop a similar habit, although the owner neither rewarded nor encouraged the dog's behaviour. This phenomenon was interpreted as a form of social mimetic

processes that might contribute to the synchronisation of group activities and to the manifestation of cooperative actions between dog and owner. This suggests that dogs are not only skilful in forming associations between human behavioural cues and some motor responses, but may show an ability to understand the constituents of the problem situation in the form of recognizing social-behavioural rules.

In the present study we used a traditional object permanence paradigm (Piaget 1954) to investigate whether dogs' and human subjects' behaviour can be explained in terms of their ability to identify and use social rules that are formed by the interaction with the experimenter during the consecutive object hiding and search tasks.

When solving an object permanence task subjects' performance could be based on a number of different cognitive capacities such as the ability (1) to represent an object mentally at least during the duration of the test; (2) to use appropriate deductive inferences; (3) and to use associative learning and local rules or cues. The presence of appropriate motivation to solve the task (4) could also be an important factor in the successful solution of the problem and there is an additional factor that may play an important role in determining subjects' performance; (5) to identify and use social rules which are formed by the interaction with the experimenter during the testing procedure (see Topál 2009 for a review).

In the object permanence paradigm subjects are presented with a number of trials during which the experimenter hides an object behind one of the screens in more or less complicated ways. At the beginning of the hide-and-search trials subjects (children or animals) are ignorant regarding the specific goals of the situation (i.e. they should focus on the hiding procedure in order to get relevant information on the baited location). Many assume that repeated trials lead to subjects' gradual learning to use relevant "local rules" or cues when search for the hidden bait (Gagnon & Doré 1993). However, if a subject considers the consecutive trials as a social situation, which involves a more or less complex game regulated by a social rule-system (e.g., "he hides, I search"), then not only the represented location of the object, but also the observed behaviour of the experimenter and the subject's tendency to form expectations about the social rules of the task may significantly influence the observed performance. In other words, the search behaviour may not only be guided by the subject's mental representations but may also be influenced by its ability to recognize and obey social rules.

The present study was therefore designed to demonstrate that social rules identified by the dog/human subjects during the consecutive trials of an object permanence test may have an independent influence on their performance in case of both children and dogs.

4.3.1. EXPERIMENT V/1.

METHODS

Subjects

Since active and volunteer participation in trials was essential, some subjects were previously excluded because of insufficient motivation or attention. 6 children and 11 dogs proved to be resistant: they refused to search or retrieve the object during the introductory shaping trials. After their exclusion, our two groups of

subjects consisted of 24 preschoolers (14 girls and 10 boys between 4-6 years of age; mean age±SD: 5.4±0.6) and 19 dogs (8 females and 11 males between 1.5-7 years of age; mean age±SD: 3.2±1.5) of five different breeds (11 Belgian shepherds, 3 Labrador retrievers, 4 Golden retrievers, 1 Dobermann pincher).

Experimental procedures

The different conditions of the experiment were carried out in environments moderately familiar to the subjects: children were observed in a room of their nursery school, while the dog subjects were tested in an enclosure at the training school that they attend at weekends together with their owners. Three green plastic screens (frontal side: 40x60 cm) were placed along a semicircle and a plastic nontransparent flower-pot (20 cm deep, 15 cm in diameter) was used as a container. An experimenter, a cameraman, an assistant and the subject were in the room during the trials. The assistant was the owner for the dogs and a familiar nurse for the children (Figure 4.3.1.1).

Route of the experimenter 2.screen Subject Figure 4.3.1.1. Schematic representation of the experimental arrangement.

Both dogs and children were treated identically; preschoolers did not receive any specific instructions about the nature of the task before the trials of the experiment began. "We shall perform an experiment, please act as you feel appropriate!" they were told. After entering, the subjects were allowed to explore the environment for a minute. The assistant showed several different objects to the subject, trying to arouse interest in them. The target object to be used was either a small rubber bear, a plastic dog, a plastic baby doll or a small ball depending on which one of these the subject showed most interest in. Then the assistant got the subject to sit down in the middle of the circle. The experimenter caught the subject's attention with the target object in hand and then proceeded to place the object into the container. The experiment consisted of three phases of trials: 'shaping', 'no object' and 'game'.

Shaping trials (6)

During the introductory shaping trials six successive visible displacements were administered. Experimenter went around behind the first screen, out again, behind the second, out again, behind the third, out again with the object made visible between screens provided it was still in the container. Care was taken that the subject was clearly attending to and following each step of manipulation. In half of these trials (during the second, fourth, and sixth trials) the experimenter visited all the three screens sequentially but the object remained in the container throughout. In the other half of the trials (i.e., during the first, third and fifth trials) while walked behind the screens 1, 2, 3 in consecutive order, the experimenter randomly left the object behind one of them. When the experimenter returned, he placed the container in front of the subject for inspection and then the assistant called upon the subject to search for and retrieve the toy. If the object was retrieved, the subject was praised by the assistant.

'No object' trial (1)

The shaping trials were followed by a modified version of the standard successive invisible displacements task. This was similar to the shaping trials in which all the three screens were visited, except that now the displacements of the target object were invisible: i.e., the content of the container was not revealed between visiting the screens. In fact, the target object was not left under any of the screens as the experimenter, while he was hiding the container behind one of the three screens, placed the toy surreptitiously in his pocket. Therefore at the end of this trial, not only the container presented, but also all of the three hiding screens were empty. When experimenter returned, the empty container was shown to the subject, and the assistant allowed the subject move freely without, however, giving any specific instructions to search for or retrieve the object. (Subjects were prompted with the Hungarian word "Mehetsz" - "you may go", but without any additional instructions or gestures to encourage search.) So the subject was allowed to search some or all of the containers freely for a minute or, in fact, to engage in any other type of behaviour, while his/her/its performance was videotaped. After a minute the hidden toy was presented to the subject by the experimenter. It was taken visibly from his pocket, so subject could realize that s/he/it was fooled.

'Game' trial (1)

This was identical to the 'no object' trial, except for the fact that before the trial began, the experimenter gave the object clearly visibly to the assistant, who first caught the subject's attention with it, and then put it in his/her pocket. So, during this condition the real location of the object was obvious and known to the subject throughout the whole procedure. Then the experimenter went on to perform the same series of acts of hiding behind the screens as in the no object condition, this time, however, with an empty container in hand.

This control condition was designed to determine, whether the experimental procedure was interpreted by the subjects as an object-oriented task with the aim of finding and getting the target object, or as a game regulated by social rules that the subject needs to follow (see Table 4.3.1.1 below). The behaviour of the subjects in each condition was video recorded for later analysis.

Data collection and analysis

In the 'Shaping', 'No Object' and 'Game' conditions different aspects of subjects' behaviour were recorded and analysed. During the 'Shaping' trials only the "Number of errors" was recorded (i.e. if the first choice was an empty screen) and compared.

Subjects' performance during the 'No Object' trial was evaluated both on the basis of their "First choice" (i.e. the location of the screen inspected firstly) and the "Order of visited screens". Subjects were scored on the basis of whether they show systematic/sequential search behind all the three screens (score: 1) or a nonsystematic search (score 0).

In the 'Game' condition, however, the "Number of subjects performing a search" was recorded. Moreover, in case of dogs the "Time spent with examining the screens" (i.e. the time spent with exploring the ground behind the screens – sec.) and the "Number of glances at the Owner" (i.e. number of direct head orientations towards the owner) were also recorded.

RESULTS & DISCUSSION

Shaping phase

During the successive visible displacements, a trial was considered correct if the subject's first choice was the screen containing the object or the container when the object remained in it $(2^{nd}, 4^{th} \text{ and } 6^{th} \text{ trials})$. The search pattern of subjects was analyzed for the trials on which the object was hidden $(1^{st}, 3^{rd} \text{ and } 5^{th} \text{ trials})$. When shown the empty container, the children typically glanced into it and set out to search the screens. The dogs also made a quick visual inspection of the container, but most dogs also sniffed it as well and then went on to the screens. Both dogs and children could find the object within 15 s in all shaping trials. Regarding their first choice, children committed significantly less error than expected by chance (chance expectation: 2 errors out of 3 trials). The difference from 0.66 chance expectancy as observed across individuals was highly significant (Sign test, p < 0.0001; nobody made more than 2 mistakes and there were only 5 ties). Dogs also made significantly less mistakes, however in this case, the difference from chance expectancy was not so highly significant (Sign test, p = 0.021; 1 dog made more than 2 mistakes and there were 9 ties).

There are significant differences between dogs and children (Mann-Whitney U = 113, p = 0.003): dogs made more mistakes (in 29 out of 57 trials - 50.8%) during the shaping trials than preschoolers (in 18 out of 72 trials -25%).

On Trials 1, 3, and 5, all subjects searched until they eventually found the target object. Thus, one of the two possible errors that subjects could make on Trials 3 and 5 was the classic A-not-B error of returning to the place in which the object was found on the preceding trial of screen hiding. Errors on Trials 3 and 5 were examined to determine the extent to which subjects were prey to this error form. Of the 12 errors made by children, 5 (42%) were A-not-B errors. Of the 23 errors made by dogs, 16 (70%) were A-not-B errors. In the latter case, the difference from 50% chance expectancy as observed across individuals (11 favouring, 5 not, and 3 ties) approaches significance (Sign test, p < 0.11).

Performance of subjects on Trials 2, 4, and 6 is notable. On these trials, the object was shown to remain in the container. None of the children and only 2 of the

dogs ever went on to check behind the screens once shown that the object was still in the container. This was a clear and sensible contrast to the motivated search on Trials 1, 3, and 5 following disclosure of the empty container.

'No object' condition

Since the subject has no information as to which one of the three screens may be hiding the target object, he/she/it should consider each screen as an equally probable hiding location and so would be expected to sequentially search behind each of them.

Accordingly, a representational hypothesis predicts that a subject, who has a fully developed object permanence capacity, should search systematically behind all the three screens during this condition. Indeed, in accordance with this prediction, most of the preschoolers and the majority of the dogs performed a full and systematic search of all three screens. The percentage of systematically inspector subjects in the three experimental groups did not differ significantly (dogs -68%, children: 91%, Fisher exact test p > 0.1)

Note that since the probability of each screen being the actual hiding place for the object is equal, the representational model provides no reason to prefer any one of them. However, both groups exhibited clear screen preference as their first choice for inspection (difference from random distribution, dogs: $\text{Chi}^2(2) = 7.70$, p < 0.05; preschoolers: $\text{Chi}^2(2) = 9.75$ p < 0.01). Most of the dogs (12/19) inspected first the screen that was visited last; as if they followed the local rule of 'go to the screen last manipulated by the experimenter'. The preschoolers searched systematically either in a backward direction (13/24, i.e., similarly to dogs, starting from the last visited screen and proceeding backwards) or in a forward direction (10/24) starting from the first screen visited by the experimenter, as if they acted according to the local rule of 'follow the experimenter's route'. The preponderance of both groups to begin with an outside (vs. the middle) screen may also reflect the influence of some evaluation of least effort in composing a search path.

'Game' condition

Since in this condition no object was hidden into the container visiting the screens, based on the representational hypothesis no search behaviour behind the screens was expected. This should be so as long as the task is interpreted as being solely about finding the hidden object and assuming that the subjects are able to remember by the end of the trial where the object was last seen (i.e., in the owner/assistant's pocket). Nevertheless, a considerable number preschoolers (12/24; 50%) and dogs (14/19; 73.7%) performed a search behind the screens despite the fact that earlier they had witnessed the placing of the object into the pocket of the assistant.

However, there were important differences between certain aspects of the search behaviour elicited in the 'No object' condition versus the 'Game' condition, respectively. Thus, during the 'Game' condition both dogs and children inspected the screens systematically less frequently than during the 'No object' condition (Wilcoxon matched pairs test: Z(19) = -3, p = 0.0027 for dogs; Z(24) = -3.05, p = 0.0023 for children).

Following the 'Game' condition the preschoolers were asked about the real location of the object which they could correctly recall in all cases. This indicates that the search behaviour observed in such cases was *not* aimed at get the object the target object. More importantly, a comparison of the dogs' behaviour during the 'No

object' and 'Game' conditions, respectively, suggests that they were also aware of the location of the target object. Figures 4.3.1.2. & 4.3.1.3. show that compared to the 'No object' condition, during game condition searching dogs spent significantly less time with examining the screens (two sample t-test: t(26) = 4.05, p < 0.001) and during search they glanced more frequently at their owner (two sample t-test: t(26) = 3.32, p = 0.0026) in whose pocket the object really was. Therefore it seems that the behaviour of both dog and human subjects in the game condition was the result of identifying and following a social rule of a game rather than the consequence of lacking appropriate representational capacity.

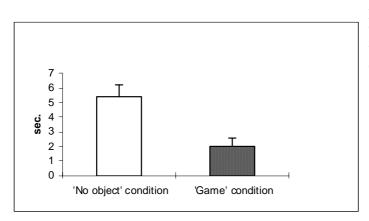


Figure 4.3.1.2. Time spent with examination of the screens (mean+SE) in the dogs during the 'No object' and 'Game' conditions.

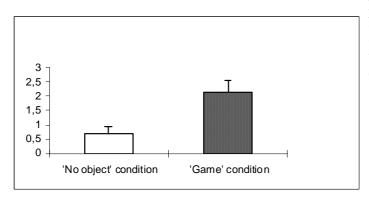


Figure 4.3.1.3. Number of glances at the owner (mean+SE) by the dogs during the 'No object' and 'Game' conditions.

What kind of social rule determined the subjects' search behaviour in the game condition? Based on their search behaviour subjects could be categorized into 3 main groups. In the game condition some of the subjects seem to have assumed that the task is about finding and retrieving the target object. These subjects (21-50% of all subjects – see Table 4.3.1.1) *did not* search behind the screens during the game condition, as they probably knew well that the target object was at a quite different location, but instead they stayed close to the ball orienting towards the owner/assistant. In contrast, the other subjects did search the screens; some of them, in fact, exhibiting systematic sequential search behind all three screens starting from the first screen visited by the experimenter (Rule II), while others showed a more diffuse search pattern (Rule III, see Table 4.3.1.). These latter subjects searched not only behind some of the screens, but other places in the room as well, irrespective of the real location of the target object.

It seems that in the 'Game' condition dog/human subjects' search behaviour was guided by different hypothetical rules in comparison to the 'No object' condition. During the 'Game' condition none of the subjects produced the kind of systematic

search that starts at the last screen manipulated by the experimenter, even though such a search pattern was observed quite frequently both in dogs and preschoolers during the 'No object' condition (i.e., when they believed that the object was indeed hidden under one of the screens). This finding suggests that the "forward sequential search" pattern observed in the game condition was not driven by the aim of finding the target object, but rather, it was generated by the social rule to "follow the experimenter's route".

	Rule I.	Rule II.	Rule III.
Dogs (N = 19)	25	21	54
Children (N = 24)	50	29	21

Table 4.3.1.1. Proportion of subjects (%) following the different hypothetical rules during the game condition. Rule I: "get the object" - behaviour: no inspection; Rule II: "follow the experimenter's route" - behaviour: "forward", sequential search; Rule III: "produce search behaviour" - behaviour: scattered exploration

4.3.2. EXPERIMENT V/2.

In the first experiment we found that dogs, similarly to children, tended to show searching even when the ball was obviously not hidden behind the screens. This behaviour, a "habit" having no obvious goal, has probably been developed as the result of the experimenter's behaviour demonstrations (i.e. performing the same behaviour sequence repeatedly upon shaping trials). The question, however, that why a large proportion of dogs in the above experiment decided to choose an "aimless" search between/behind the screens instead of showing a goal oriented behaviour (i.e. trying to get the ball from its well known place) needs for further clarification. The "social rule" hypothesis described in the first experiment leads to specific predictions with respect to the dogs' behaviour.

First, a basic precondition for the development of any "social-behavioural" rule in a hide-and-search task is, that the dog should focus not only on the movement of the object behind the screens upon hiding but on the *behaviour* of the human demonstrator too. That is, eliminating the social nature of the hide-and-search task (i.e. when human is not involved in the hiding process) dogs should not show search behaviour in a situation where the reward is not hidden ('Game' condition).

Moreover, in a social "version" of the hide-and-search task the emergence of rule following behaviour in the dog (i.e. willingness to search in a situation where no reward is hidden) can be facilitated by the repeated and stereotypic nature of the demonstrated hide-and-search tasks and by the increase of non-relevant elements in the demonstrated action sequence (i.e. intricate behaviours upon hiding the ball).

In the following experiment we aimed to study the aforementioned predictions and experimental groups were also designed to exclude the possibility that the emergence of search behaviour when there is no hidden reward is due to the dogs' limitations in working memory.

METHODS

Subjects

Fifty-four adult pet dogs of different breed participated in this experiment. The dogs and their owners were recruited on a voluntary basis in dog training schools. The only criterion for selection was that the dogs had to be highly motivated to play with a tennis ball, therefore prior to the experiment the owner was asked to perform 3–4 retrieval task with his/her dog.

Experimental procedures

Three screens (frontal side: 40×25 cm, green plastic) were staged in line, 1 m distance in between. There was a stool 3 m behind the middle screen. Dog, owner and experimenter stood at a distance of 5 m in front of the middle screen. A Panasonic DV camera stood on a tripod 5 m behind the first screen.

The experimental procedure consisted of two phases: Shaping trials (6) and Game trial (1). Groups were designed to analyse the effect of different conditions (Shaping trials) on the dogs' willingness to show "social-rule following" in the subsequent 'Game' trial. The following 5 experimental groups were tested:

Simple route, pretended hiding without ball (Simple – No Ball group) (N = 11, 7 males, 4 females, age = 2.5 ± 1.0 ; 5 Belgian shepherds, 1-1 German shepherd, Airdale terrier, Dachshund and 3 mongrels)

'Shaping': During the first shaping trial the experimenter drew the attention of the dog to the ball, and went to the first screen while the ball was constantly visible in her right hand. Then she crouched behind the screen, put the ball down, and returned, showing that her hand is empty. The owner said: "Bring it to me!" ("Hozd!" in Hungarian) only once. After the dog retrieved the ball the owner gave it back to the experimenter. Then the experimenter hid the ball behind the second screen and finally the same sequence of actions was repeated for the third screen. The whole procedure was repeated (altogether 6 trials).

'Game' trial: The experimenter caught the dog's attention with the ball in her hand and then slowly placed it into the owner's palm, who put it behind his/her back. Then the experimenter went to the first screen, constantly showing her empty hands, and crouched behind the screen, but did not put down her hands so the dog could always see them. After it she went back to the dog and the owner let the dog free while saying: "You can go!" ("Mehetsz!" in Hungarian). The dog was allowed to move freely for 30 sec while the owner remained at his/her predetermined position and did not give any gestural or verbal signal to the dog.

Intricate route, pretended hiding without ball (Intricate – No Ball group) (N = 11, 6 males, 5 females, age = 2.3 ± 1.1 ; 5 Belgian shepherds, 1-1 German shepherd, Griant schnauzer, Leonberger, Golden retriever and two mongrels)

'Shaping': During the first shaping trial the experimenter drew the attention of the dog to the ball, and before putting down the ball behind the first screen, she first walked round the stool behind the screens, while the ball was constantly visible in her middle-held right hand. Then she crouched behind the screen, put the ball

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down, and returned, showing that her hand was empty. The owner said: "Bring it to me!" ("Hozd!" in Hungarian) only once. After the dog retrieved the ball, the owner gave it back to the experimenter. The experimenter repeated the process with screens 2 and 3. Six such shaping trials have been performed.

'Game' trial: The procedure was identical to that used in Simple - No Ball group.

Intricate route, pretended hiding with ball (Intricate – Ball group) (N = 11, 9 males, 2 females, age = 2.9 ± 2.1 ; 4 Belgian shepherds, 3 German shepherds, 1-1 Collie, English setter, Labrador, Boxer)

'Shaping': The procedure was identical to that of described in Intricate - No Ball group.

'Game' trial: The procedure was identical to that described for Intricate - No Ball group, except that the experimenter took the route with the ball in her hand and gave it to the owner only after visiting the screens.

Intricate route, pretended hiding with ball, 25 sec delay (Intricate – Ball – Delayed group)

(N = 10, 3 males, 7 females, age = 2.4 ± 2.4 ; 2 Belgian shepherds, 1-1 Sheltie, Airdale terrier, Hungarian vizsla, Cocker spaniel, Mudi and three mongrels)

'Shaping': The procedure was identical to that described in *Intricate – No Ball* group.

'Game' trial: The procedure was identical to that described in *Intricate – Ball* group, except that the owner did not release the dog when the experimenter returned, only after 25 sec elapsed (that was the mean time of walking the path by the experimenter).

Throwing the ball group

(N = 11, 6 males, 5 females, age = 2.6 ± 1.6 , 5 Belgian shepherds, 2 German shepherds, 1-1 Hungarian vizsla, Pumi, Mudi and a mongrel)

'Shaping': An adult man sat on a stool during the experiment. The experimenter threw the ball to the man, who rolled it behind the first screen. The owner said: "Bring it to me!" ("Hozd!" in Hungarian) only once. After the dog retrieved the ball the owner gave it back to the experimenter. Then the ball was hidden behind the second screen in the same way and finally the same sequence of actions was repeated for the third screen. The whole procedure was repeated (altogether 6 trials).

'Game' trial: The experimenter threw the ball to the man sitting on the stool who threw it back to the experimenter. Then she caught the dog's attention with the ball in her hand and slowly placed it into the owner's palm, who put it behind his/her back. After it the experimenter commanded the dog: "You can go!" ("Mehetsz!" in Hungarian).

According to the aforementioned predictions we expect that those dogs should show the highest tendency to perform search behaviour in the test trial (i.e., when the ball is not hidden) who witness an "intricate" hiding route and the pretended hiding is demonstrated without ball (*Intricate route, pretended hiding without ball* group). In comparison to these subjects, when the hiding route is more

goal-directed (*Simple route, pretended hiding without ball* group) or the pretended hiding is shown by the experimenter with the ball in her hand (*Intricate route, pretended hiding with ball* group), dogs should show a weaker tendency to perform search behaviour in the test trial ('Game' condition).

Moreover, in a "nonsocial" version of the hide and search task, that is, when no human is involved in the repeated hidings, dogs should not show search behaviour in the situation where the reward is not hidden (*Throwing the ball* group).

RESULTS & DISCUSSION

Shaping trials

We analysed the latency of getting the ball in the repeated trials (within subject factor) and the experimental group (between subject factor) with mixed ANOVA for repeated measures to the within subject factor. Further, we used Student-Newman-Keuls post hoc tests (between group comparisons). The groups showed significant differences (dogs in 'Throwing' group get the ball sooner than the others; $F_{4,49} = 5.864$, p = 0.001), but neither the repeating nor the interaction proved to be significant (F(4,49) = 1.53, p = 0.181 and F(5,49) = 0.282, p = 0.888 respectively).

Regarding the number of erroneous choices (an error was recorded if the dog visited a non-baited screen or the stool before the baited screen) we found significant differences between groups. Dogs in the *Throwing the ball* group made significantly less errors than subjects in the *Simple – No Ball* and *Intricate – No Ball* groups (Kruskal Wallis test with DUNN's post hoc test: $chi^2 = 21.165$, p = 0.0003). It seems that dogs could focus on the visible displacement task better when the ball was thrown between the target locations instead of transferring it by the human.

'Game' trial

The focal question regarding subjects' behaviour in the 'Game' trials was whether dogs leave their owner (who holds the ball) and perform search behaviour around the experimental area or remain in the close vicinity of the owner. Subjects leaving the vicinity of the owner (< 1 m) within 5 seconds after the command ("You can go!") and starting the search were categorized as "Searchers". We should note that in the 6^{th} shaping trial each dog (in all groups) was categorized as "Searcher" (i.e., left the owner and retrieved the ball). In the 'Game' trial, the majority of dogs (64%) in the *Intricate – No Ball* group were categorized as "Searcher". In this case the number of "Searcher" individuals in the 'Game' trial did not differ significantly from the frequency of searchers in the 6th shaping trial (McNemar test, p = 0.125).

The same comparisons show, however, that subjects' behaviour significantly changed in all of the other groups as the majority of them did not leave the owner (i.e., the ball). That is, when the hiding route of the human demonstrator was goal-directed ($Simple - No \ Ball \ group$), only 27% of the subjects were categorized as "Searcher" in the 'Game' trial (comparison with the last shaping trial: McNemar test: p = 0.008).

Similarly, when the pretended hiding in the 'Game' trial was demonstrated with the ball in hand (Intricate - Ball group), only one third of the dogs (36%) performed searching behaviour in the 'Game' trial (McNemar test: p = 0.016) and this ratio was only 10% when the dog had to wait 25 seconds after the demonstration (Intricate - Ball - Delayed group; comparison with the last shaping trial – McNemar test: p = 0.004). This latter observation suggests that dogs could keep the location of

the ball in their working memory. Moreover, when the hiding process was nonsocial (*Throwing the ball* group) none of subjects searched in the 'Game' trial (i.e., all dogs stayed next to the owner – McNemar test: p = 0.001)

All of these suggest that dogs left the owner (and the ball) more frequently when previously they had been trained for a hide-and-search task using a more sophisticated way of object hiding, provided that the experimenter accomplished the test trial without the ball in her hand. It seems that the ball in the hand during the test trial (pretended hiding) maintained the dogs' attention on the ball and therefore dogs preferred the "get the object" strategy (waiting for the ball near the owner orientating to her/his) when they were allowed to choose. Searching when the reward is not hidden behind the screens was not due to working memory problem as dogs could recall where the reward had been seen even after 25 sec (i.e., 90% of the dogs in the *Intricate – Ball – Delayed* group did not leave the owner in the test trial).

As predicted, when the social-behavioural component of the hide-and-search task was removed (*Throwing the ball* group), dogs seemingly favoured the "get the object" strategy versus "social-behavioural" rule following (i.e., search behaviour) in the game condition.

4.3.3. STUDY V. GENERAL DISCUSSION

Object permanence, as one of the major achievements of early cognitive development, has been assessed by a variety of experimental methods (Piaget 1954) and performance on such tasks has been measured on a standardized scale (Uzgiris & Hunt 1975). Success in the invisible displacements tasks by two-year-old infants and older human subjects has typically been interpreted as indicating a mature mental capacity to represent the permanent and independent existence of objects and an ability to use deductive inference to mentally reconstruct the invisible changes in a displaced object's spatial position. However as Piaget, himself, repeatedly pointed out, solving the invisible displacements task does not necessarily imply the use of a mental representational model generated by deductive inference (Piaget 1954). In fact, as recent studies using different nonhuman species demonstrate, the problem can be successfully solved by non-representational means as well such as associative learning and the reliance on local rules or cues (for a review see Gomez 2005).

In this study we have hypothesized that successful performance on such tasks may also be influenced by an additional factor, namely, the subjects' propensity to obey social rules of a task that is interpreted as a behavioural game. According to this view, the subsequent trials of different hiding procedures can be construed by the subjects as a social game regulated by a behavioural rule system that they infer from the experimenter's actions. The present study was designed to demonstrate the effect of such social rules on the performance of dogs as well as humans in an object permanence task. The paradigmatic element of our experiments is that we used a shaping procedure involving a series of visible object displacements (i.e., hide-andsearch tasks) to familiarize dogs and children with the experimental situation. In accordance with former studies (e.g. Wood et al. 1980; Gagnon & Doré 1992) we found that not only preschoolers but also dogs fulfilled the standard criteria for successive visible displacements tasks showing results significantly above chance performance in the shaping trials. However, as the findings in "Game" condition indicate, systematic sequential search is not a sufficient criterion for demonstrating representational understanding of object permanence, as such a search pattern

('forward' sequential search - see Table 4.3.1.1.) has also been observed in a significant number of subjects even when no object was hidden under the screens and the subjects were demonstrably aware of the actual location of the target object. We suggest, therefore, that systematic search in the game condition can be seen as subjects' susceptibility to interpret the hide-and-search tasks as a situation involving rules of a social game.

The observed differences in the behaviour shown in the 'No object' and 'Game' conditions (Experiment V/1.) gives further support for the assumption that dogs and children are sensitive to the 'game-like' nature of the situation. While even dogs have shown some degree of representational understanding of object permanence in the 'No object' trial, they performed less goal-directed behaviour in the 'Game' condition ('aimless' search despite the fact that the location of the reward is well-known).

Although the first experiment of this study has shown that both humans and dogs created and followed some sort of a social rule in the context of the object permanence test, but did not reveal the underlying mechanisms. Human subjects could give follow-up comments on their own behaviour, but these explanations did not point out exactly, what kind of factors urged them to produce search behaviour. Usually all they said was that they thought they should search because of the behaviour of the demonstrator. The forward sequential search pattern observed in the 'Game' condition suggests that the *way of hiding* behaviour (in the Shaping trials) is probably the key-component for the emergence of the "aimless" search behaviour (i.e., obeying social rule) in the subsequent 'Game' trial.

Unlike human subjects dogs of course could not give verbal explanation for their behaviour, therefore we decided to reproduce the findings using a simplified shaping procedure, where we could systematically manipulate and observe the effect of the special hiding methods. According to this, and in line with the approach proposed by de Waal (1991b) for studying the nature of social rules, the plausibility of 'social rule' hypothesis in dogs can be studied through the direct analysis of its specific predictions. One of these is that the elimination of the social component should lead to at least two consequences regarding the dogs' behaviour performance.

First, dogs should perform better in the ball-retrieving task because they do not divide their attention between the (intricate) behaviour of the human demonstrator and the actual position of the target object.

Second, in the 'Game' condition, there is no reason to perform search behaviour around the screens provided that the dog can recall that the ball is in the hand of its owner. Our findings supported these assumptions: dogs did not visit the non-baited screens during the shaping trials, and did not leave the owner in the 'Game' trial if the human demonstrator was not involved in the hiding procedure.

Furthermore, Experiment V/1. has raised another issue. Namely, the human demonstrator performed several salient, but functionally not relevant behaviours during the shaping period. She visited each screen in the same sequence no matter which one was baited actually and in the 'Game' condition, she performed a complete hiding ritual without the ball in her hand. This could lead to the prediction that the functionally non-relevant behaviours of the human demonstrator (in shaping and pretended hiding trials) could be a further important factor for the emergence of rule following behaviour in dogs. Results of the second experiment support the aforementioned predictions. The tendency to perform "aimless" search behaviour was highest among those groups, which could see a more intricate hiding route during the shaping trials and 'hiding with empty hands' in the subsequent trial. One

may assume that this was due to the dogs' limitations in working memory, however, results (with the 'delayed' group) do not support this possibility. These findings coincide with our earlier observations (Kubinyi et al. 2003), where after seeing a systematically recurring exposition of a functionally non-relevant, aimless, but stereotype detour by the owner, dogs tended to take over the habit.

In sum: it seems that the sequential visible and invisible displacement tasks, that were originally designed to demonstrate a representational understanding of object permanence, may be interpreted by subjects not only as object hiding and finding tasks, but, alternatively, as social-behavioural games of different sorts that may contribute to the subjects' systematic search performance. Therefore, successful performance on such tasks may be based on qualitatively rather different underlying mediating mechanisms, and so it should not be interpreted exclusively as indicating a representational understanding of object permanence, and an ability to make deductive inferences.

4.4. THE SYNCHRONIZATION DOMAIN OF DOG BEHAVIOUR COMPLEX: SUMMARY OF RESULTS.

Synchronization between group-mates can be manifested at different levels (physiological, motivational/emotional and behavioural alignments) and is supposed to be essential for group cohesion. Interactional synchrony at the behaviour level is the most obvious one. Dogs' ability to use human behaviour as a cue for selecting functionally similar behaviour (imitative learning – see STUDY IV; as well as Miller et al. 2009; Huber et al. 2009) is an important underlying mechanism by which interactional synchrony between dogs and humans can be achieved.

In this chapter we have also pointed out that dogs' behaviour can - at least partially - be explained in terms of rule following when in an object permanence task (STUDY V). For the dog, the function of human demonstration (hiding an object repeatedly) is probably not transferring knowledge per se but transferring those behaviour actions that can lead to effective behavioural synchronization. Dogs seem to be sensitised to the recurring, but cognitively and causally opaque behaviour of humans. This skill can be seen as a behaviour adaptation to a complex human environment which might contribute to the emergence of a close relationship with a different species. The willingness to follow social rules in dogs could serve as the scaffolding on which many forms of complex social behaviour between dogs and humans can develop. The apparent flexibility of dogs' behavioural responses to a stranger's approach in STUDY III further supports the notion that dogs have some ability to show emotional and behavioural response in accordance with the human's attitude. Such behavioural-emotional synchronization is supposedly a bi-directional process. Interactional synchrony is most likely to develop if the human attends carefully to the dog's emotional and attentional state.

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 synchronisation of group activities as members of the group can act on the basis of the same knowledge. This could make interactions between companions more easygoing and more efficient.

It is also worth mentioning that synchronisation between dog and human can also take place "under the surface". 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). As bodily contact in the form of 'social grooming' is a dominant behaviour for expression empathy in humans, dogs could have been selected for similar tendencies. It seems that establishing a positive feedback system, oxytocin plays an important role in the formation of human-dog relationship. This anxyolitic neuropeptid is released in response to physical contact (Uvnas-Moberg 1997) or other social cues (e.g. gaze) and plays an important role in modification of behavioural response to stress situations. Mutual gazing with the dog increases the owner's urinary oxytocin levels, which is an indirect signal of the increased production of this hormone in the brain (Nagasawa et al. 2009). Others found that dog-owner social interaction significantly increases the plasma oxytocin concentrations in both partners thus supporting the mutual relaxing effect of petting (Odendaal & Meintjes 2003). These findings open the door to understanding of physiological, emotional and behavioural synchronization between individuals of such evolutionary distant species like man and dog and give some further support for the idea that dogs have undergone selection for living in human groups.

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CHAPTER 5.

CONSTRUCTING COMMUNICATION

The above two chapters (3 & 4) provided an overview of the available evidence concerning parallels between the Dog- and Human Behaviour Complexes in cases of increased sociality, multi-level synchronization and we also presented some additional empirical findings about these two domains of social cognition in dogs. The present chapter, however, will focus on a different aspect of the dog social cognition: the constructive character of interspecific communicative behaviour.

Generally speaking communication involves complex constructive activities for both participants (signaller and receiver). This is also true for such 'low-level' nonverbal forms of communication like gestural exchange between dogs and humans. During the past decade numerous investigations have revealed that, similarly to mother infant exchange of information, dog human communicative interaction can be described as a step-by-step constructive process based on a set of specific skills in both participants. Namely, for the effective communication the 'initiator' has to provide cues expressing its communicative intent toward the potential recipient (e.g. via establishing eye contact). Next, the recipient should be able to identify the context as being communicative interaction, and should focus its attention on the signaller. Then the informant has to specify what (s)he is informing about (e.g. using gaze shifts or pointing) and has to manifest the message (knowledge) in a manner and form that makes obvious for the receiver what is the relevant information about the referred object (e.g. fetch it!). Finally, both parties have to adjust their behaviour to cases when the communication fails, and should aim by different means to achieve their goal of communicating.

It has been reported that, dogs show special responsiveness to human communicative signals (Miklósi & Soproni 2006). Dogs like 18-month-old infants, and unlike wolves and apes, are skilful users of various forms of human directional gestures (e.g., Lakatos et al. 2009). These findings, in agreement with other studies, raise the possibility that dogs' understanding of human ostensive referential communication is more flexible than was formerly thought and shows functional similarities to the human infants' corresponding skills. Our aim in this chapter is therefore to provide further insight into the characteristics of human infant-analogue social competence in dogs.

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STUDY VI. SENSITIVITY TO CUES THAT SIGNAL THE HUMAN'S COMMUNICATIVE INTENT AND UNDERSTANDING THE REFERENTIAL SIGNIFICANCE OF VISUAL ATTENTION*

Abstract

Dogs' ability to recognise cues of human visual attention was studied in two different experiments. The first one was designed to test the dogs' responsiveness to their owner's tape-recorded verbal commands (Down!) while the Instructor (who was the owner of the dog) was facing either the dog or a human partner or none of them, or was visually separated from the dog. Results show that dogs were more ready to follow the command if the Instructor attended them during instruction compared to situations when the Instructor faced the human partner or was out of sight of the dog. However, dogs showed intermediate performance when the Instructor was orienting into "empty space" during the re-played verbal commands. This suggests that dogs are able to differentiate the focus of human attention.

A second experiment was aimed at studying the question whether dogs' responsiveness to human directional gestures is associated with the situational context in an infant-like manner. Borrowing a method used in infant studies, dogs watched video presentations of a human actor turning toward one of two objects and their eye-gaze patterns were recorded with an eye tracker. Results show a higher tendency of gaze following in dogs when the human's head turning was preceded by the expression of communicative intent (direct gaze, addressing). This is the first evidence to show that eye-tracking techniques can be used for studying dogs' social skills and the exploitation of human gaze cues depends on the communicatively relevant pattern of ostensive and referential signals in dogs. Our findings give further support to the existence of a functionally infant-analogue social competence in this species.

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Téglás, E., Gergely, A., Kupán, K., Miklósi, Á., Topál, J. (2012). Dogs' gaze following is tuned to human communicative signals. Current Biology, 22: 1-4.

^{*}Based on:

INTRODUCTION

The dogs' sensitivity to human gestural cues involving cues of visual attention has been reported in many independent studies using food choice tasks (see Miklósi & Soproni 2006; Miklósi 2007, for reviews). Additionally, dogs learn very fast to utilise eye cues only in such tasks (e.g., Miklósi et al. 1998). These studies suggest that dogs are able to use broad range of human given cues—even novel ones—in social situations and they are more skilful in this respect than primates. When using human visual cues to find hidden food, the superior performance in dogs has been confirmed by direct (Hare et al. 2002) and indirect (Soproni et al. 2001; Povinelli et al. 1999) comparisons. These studies concluded that unlike dogs, chimpanzees were not sensitive to the referential and attention components of the cues; their choice was based on the observable discriminative stimuli presented by the human informant.

Dogs' sensitivity to others' attentional cues has been investigated in some additional situations, one of which is the fetching tasks in which dogs seemed to discriminate "attentive" and "inattentive" behaviour of humans (Hare et al. 1998; Gácsi et al. 2004). As a further elaboration of these observations, Call et al. (2003) found that dogs are sensitive to whether a human is watching them or not in a situation, where dogs compete with a human over food. Dogs picked up the food more frequently when the human competitor was inattentive (eyes closed, back turned or distracted) in comparison to the trials when the human showed cues of visual attention toward them (facing the food/dog).

All experiments cited have observed how dogs respond to human cues of attention in feeding or playing contexts, in which subjects aimed to get some desirable food or play by interacting with a cooperative or a competitive human partner. However, it has not been investigated whether dogs can take into account that a human is attending to them or another human subject when communicating in a social situation where no food or toy is involved. Moreover, while recent research has provided important evidence about dogs' social communicative skills, it is still unclear whether dogs' gaze following is tuned to cues that signal the human's communicative intent (e.g. eye contact, verbal addressing).

In the first experiment dogs were commanded to perform a mildly aversive action (to lie down on command). The question was whether dogs are more disposed to omit fulfilling the command if the owner is inattentive with them than if she is looking at them. Further on, to test whether dogs have a more sophisticated sensitivity going beyond discriminating between a human's attentive and inattentive states, a third party was involved into the communicative situation. We wanted to see whether dogs are able to discriminate between the attentional focuses of a human in a triadic social situation when there are two "competing" agents present as possible targets for the command. We hypothesized that if dogs are able to perceive the focus of human visual attention and to "comprehend" the referential nature of looking, they should behave differentially in situations when their owner's verbal command is accompanied by different head and bodily orientation.

5.1.1. EXPERIMENT VI/1

METHODS

Subjects

Thirty-one adult pet dogs and their owners were recruited on voluntary basis at a dog training school. Eight dogs were excluded from the experimental group after the pretest trial because they did not respond to the owner's command and/or they displayed definite signs of stress when they were taken on leash in the experimental room (see below). After their exclusion our sample consisted of 23 adult dogs (11 males, 12 females, mean age±SD 5.7±2.6 years; 14 Tervuerens, 3 Groenendaels, 2 Boxers, 1-1 Great Dane, Mudi, Schnauzer, Collie).

Experimental procedures

Trials were recorded in a room $(4m \times 5m)$ that was unfamiliar to the dog. A big (width: 1.2 m, height: 2m) vertical screen was positioned near one side of the room. The dog, the owner (Instructor) and the experimenter (Partner) were in the room during the observations. Each condition was video-recorded and analysed later. The dogs were led into the room by the Instructor and allowed to explore the room for a few minutes. During it the Instructor and the Partner were talking to each other while they were standing at their predetermined points in the middle of the room 3m apart and facing each other. At the beginning of all trials the Instructor put the dog on leash and tethered it at a predetermined point in the corner. In this way the Instructor, the dog and the human Partner were standing so that they formed an isosceles triangle. By gently touching its body the Instructor got the dog to stand orienting towards the middle of the room, and went back to his/her predetermined position in the room. The human participants continued to talk to each other taking apparently little notice of the dog. (If the dog changed its position during the discourse, the Instructor re-positioned the dog.) After 10–20 s, when the dog was orienting towards them, they suddenly stopped talking, the Instructor took up the predetermined body orientation (see below) and gave a verbal command (Down!—'Fekszik!' in Hungarian). In the pretest trial the owner gave the instruction live but in the four experimental trials the command was given by playing back the pre-recorded verbal command of the Instructor (see below). The Partner kept on facing the Instructor without moving in all trials. Having finished instructing the dog both human participants stayed in their positions for further 5 s then the Instructor turned back to the Partner and resumed talking. The trial was terminated when the Instructor turned back to the Partner. The dog did not get any feedback (praise/scolding) at all. The behaviour of the dogs was observed in the pretest trial and in each of the four different conditions. The dogs started with the pretest trial and the order of the four subsequent playback conditions was chosen at random. There were 2–3 min breaks between the trials when the dog was allowed to move freely in the room.

Pretest trial: 'Face to face/live/'

This condition served to test the dogs' reaction to the experimental situation and whether they obey the 'Down!' command given by the owner. The content of the

verbal command was discussed with the Instructors in advance and was the same for all dogs. In the beginning of the pretest trial the Instructor and her Partner stood in the predetermined position (Figure 5.1.1.1a) and were talking while facing each other. Before giving the verbal command the Instructor turned towards the dog and looked directly at it. 'Down!' command was uttered only once but the Instructor's nonverbal gesturing was not restricted. Only those dogs (23) that lay down within 5 s after the command were involved to experimental trials.

Recording and replaying of the verbal instruction

Because we wanted to avoid the variation of the repeated command to influence the behaviour of the dogs in the different experimental conditions (see below), we have standardised the verbal cues by recording them on tape and this record was used in all further conditions. Verbal commands were tape-recorded after the pretest trial in the absence of the dog. The Instructors were told to give the 'Down!' command in the same way as in the pretest trial and to repeat it two times with noting the dog's name before the last command ('Down!' ... 'Down!!' 'dog's name + Down!!!). In this way commands had the same verbal structure for each dog with the obvious difference regarding the dog's name. The Instructors were asked to increase the imperative mode of the utterance as they proceed with approximately 3 s pauses between the repetitions. So the total duration of the verbal instructions ranged between 8 and 10 s for each dog. The tape recorder was remote controlled by the Partner in all conditions and was stopped after the command after which the dog lay down (e.g. if the dog lay down after the first command had been given, neither the second nor the third commands were played back). The loudspeaker was positioned so close to the face of the Instructor as it was possible and it was directed between the dog and the Partner's usual place. The loudness was adjusted to the human ear.

a). FACE TO FACE b). VISUAL SEPARATION

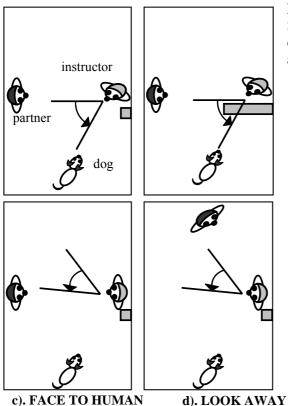


Figure 5.1.1.1. Schematic representation of the different conditions (drawn not to scale, view from above).

Experimental conditions /playback/

Face to face

This condition was identical to the pretest trial (Figure 5.1.1.1a), except that now the tape-recorded command, described above, was given.

Visual separation

The position and the behaviour of the human participants in this case were the same as in the 'Face to face' condition with the only difference, that an opaque screen was placed between the dog and the Instructor in the beginning of this trial, so the dog could not see the Instructor's body orientation (Figure 5.1.1.1.b).

Face to human partner

The starting position of the participants was identical to that in the 'Face to face' condition. After stopping their talk the Instructor, however, turned away from the Partner to the right for 2–3 s. When the command was started to replay she turned left with a definite movement in the same way as in the 'Face to face' condition but as a result of this turning now she oriented towards the human Partner (Figure 5.1.1.1.c).

Look away

In the beginning of this trial the Partner changed his position by stepping 3m sideways away from the dog. The Instructor and the Partner looked at each other and talked in this position. Before commanding the Instructor turned left toward the Partner's original place. In this way the orientation and the movements of the Instructor were exactly the same as in the 'Face to human partner' condition but she faced at empty space when the command was replayed (Figure 5.1.1.1.d).

Data collection and analysis

Great care was taken to make the non-verbal gestural behaviour of the Instructor similar across all condition. This was essential to do since in three experimental conditions ('Visual separation', 'Face to human partner', 'Look away') the uttering of the command took place in a quite unnatural situation for the Instructors. The Instructors were instructed that they should try to behave as they usually do and in a standard way in all conditions. To account for any of the potential gestural influence on the part of the Instructors, their behaviour was recorded for statistical analysis according to the following variables.

- A. Head-turning towards the predetermined direction.
- B. Body orientation towards the predetermined direction.
- C. Nodding when the command is given.
- D. Bending forward of the upper torso when the command is given.
- E. Hand-gesture (stretching out the arm and making a movement directed to down).

The presence (1) or absence (0) of these gestural cues was recorded for each repeated command in each of the experimental conditions. The average frequency of the occurrence of a given gesture was calculated for each dog–Instructor pair in each experimental condition dividing the number of occurrences by the number of command-repetitions.

In order to compare the dogs' reaction to commands uttered in the different conditions the 'Response score' was established as follows:

Score 1: The subject responded to the first 'Down!' command (i.e. started to lie down before the first repeat and finished the action before the trial was terminated (before the Instructor turned back to the Partner to resume talking (see procedure))).

Score 2: The subject started to lie down after the beginning of the second command ("Down!!") but before that of the third one ("name+Down!!!") and finished it before the trial was terminated.

Score 3: The subject started to lie down when the last command ("name + Down!!!") had been given and finished the action within 5 s (i.e. before the Instructor turned back to the Partner to resume talking).

Score 4: The dog was resistant, namely it did not lie down within 5 s after the last command had been given. Interobserver agreement was assessed by means of parallel coding of 50% of the total sample by two trained observers. Cohen's kappa for the response score was found to be 0.89.

Friedman ANOVA was used to compare the behaviour of individual dogs across conditions and similar tests were used for analysing the behaviour of the Instructors. Within-group differences were further analysed by planned comparisons (Wilcoxon tests).

RESULTS & DISCUSSION

Behaviour of the Instructors

Analyses of the non-verbal behaviours of the Instructor by Friedman ANOVA across the five experimental conditions failed to show any significant differences (head-turning, body orientation, nodding, bending the upper torso, handgesture; p > 0.05 in each case). That is, Instructors showed similar patterns of non-verbal gesturing in each of the experimental conditions, which suggests that the behaviour of Instructors cannot explain the possible condition-specific differences in dogs' responsiveness.

Dogs' response scores

Although dogs were pre-selected on the basis of their responsiveness in the pretest trials (i.e. only dogs that fulfilled live command were involved) there might have been differences in the quality between the pre-recorded command and the commands uttered by the Instructor live. Therefore, in order to analyse the effect of the application of the playback method on the dogs' reaction first we made comparison between the response scores in 'Face to face/live/' and 'Face to face/playback/' conditions. Importantly, while all dogs were ready to obey in the "live" condition (response score = 1), 6 out of the 23 dogs failed to lie down even after the repeated command in the 'Face to face/playback/' situation (scores = 3, and 4) which difference approaches significance (Wilcoxon, Z(23) = 1.88, p = 0.059). It seems that these six individuals had severe difficulties with the playback method, which is further supported by the fact that they failed to show any corresponding reaction in the other playback conditions. In order to concentrate the analysis on the direction of human attention on the dogs' responsiveness, the six non-responding subjects in the play back situations were excluded from further analysis.

The overall comparison of the response scores in the four experimental conditions resulted in highly significant differences (Friedman ANOVA, $chi^2(3)$ = 24.16; p < 0.001, Figure 5.1.1.2).

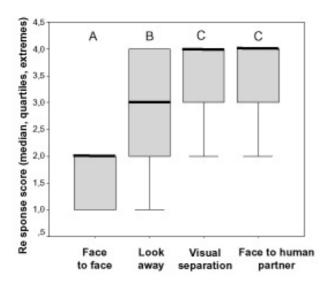


Figure 5.1.1.2.

The dogs' response score in the different experimental conditions (median, quartiles and extreme values). Different letters indicate significant differences between the conditions (p < 0.05). Score 1: prompt fulfilment after the first command; Score 2: lie down after the second command was uttered; Score 3: lie down after the third command (name of the dog+Down!!!); Score 4: command ignored.

Although all of the 17 dogs lay down in the 'Face to face' condition the majority of them proved to be resistant in the situation where the Instructor faced the human Partner or was visually separated while the command was replayed (12 and 11 out of 17). The number of dogs ignoring the command in the 'Look away' condition (7 out of 17) shows intermediate responsiveness (Table 5.1.1.1). Pair-wise comparisons showed higher responsiveness in the 'Face to face' condition than in 'Visual separation' (Z(17) = 3.25, p < 0.001) and in the 'Look away' (Z(17) = 2.97, p = 0.003) conditions. Moreover, verbal instructions were more likely ignored when Instructor oriented to the Partner than to an empty space ('Face to human partner' versus 'Look away' conditions: Z(17) = 2.15, p = 0.032). However, we failed to find significant difference between the 'Face to human partner' and the 'Visual separation' conditions (Z(17) = 0.85, p = 0.395).

Response	Face to face	Look away	Visual separation	Face to human partner
Lie down promptly				
Response score = 1	N = 6	N = 3	N = 1	N = 0
Lie down after the first repeat).				
Response score $= 2$	N = 11	N = 3	N = 3	N = 3
Lie down when its name was				
given. Response score = 3	N=0	N=4	N=2	N=2
Command ignored.				
Response score $= 4$	N=0	N=7	N=11	N=12

Table 5.1.1.1. The number of dogs that behaved according to their owner's verbal command (Down!) in the different experimental conditions

The findings of the present experiment suggest that in situations where the command is replayed by a tape recorder, the dogs' behaviour is influenced by the behavioural cues (head and body orientation, presence/absence) relating to the actual visual attention of the Instructor. Importantly, dogs are able to differentiate situations where the human visual attention is unambiguously directed to them (they fulfil the command) or to a human Partner (they ignore the command). Moreover, in a more

ambivalent situation in which the focus of the owner's attention was not unequivocal (e.g. in the 'Look away' condition the Instructor looked at a direction where there was nobody) the behaviour of the dog reflects a kind of hesitation (intermediate responsiveness). The focus of human attention was similarly unidentifiable for the dog when a screen was positioned between the dog and the 'Instructor' ('Visual separation'). In this case, however, the dogs tended to avoid responding to the command. This was probably so, because dogs either needed to see the visual cues provided by the Instructor (e.g. gestures) in order to understand the situation, or alternatively, they were non-responsive because loosing the visual contact with the owner in this strange, restrictive situation made them stressful.

5.1.2. EXPERIMENT VI/2

It is widely accepted that infants' social-communicative skills represent human specific evolutionary adaptations that allow infants to participate in dyadic communicative interactions (Csibra & Gergely 2009). Cue-based responses to ostensive-communicative and referential signals are assumed to be linked together in a specific manner which can enable even preverbal infants to benefit from referential communication directed to them. Shared attention and reflexive gaze following has been reported to be modulated by such social contextual factors as the facial emotional expressions of the demonstrator in both human (Hori et al . 2005) and non-human (monkeys – Goossens et al. 2008) subjects. However, recent evidence suggests that preverbal infants' gaze following can be triggered only if an actor's head turn is preceded by the expression of communicative intent (Senju & Csibra 2008). Such connectedness between ostensive and referential signals may be uniquely human, enabling infants to effectively respond to referential communication directed to them.

In the light of the above results (Experiment VI/1) an intriguing question is whether dogs' responsiveness to human-given gaze cues is associated with the situational context in an infant-like manner.

METHODS

Subjects

Sixty-one pet dogs of different recognized breeds (33 males, 28 females; mean age \pm SE = 48 \pm 4.4 month) were recruited to the study. Dogs were tested at the Department of Ethology, Eötvös University in a testing room specifically for dog studies. In order to be selected for this study the subject had to be naïve to the task, and older than a year. At the time of testing all owners were unaware of the hypotheses and goals of the study. Thirty-two dogs were excluded from the experiment because of inattentiveness (N = 12) or unsuccessful calibration (N = 20). The final sample consisted of those 29 dogs that provided sufficient data for the analysis of eye gaze in the cueing phase.

Sixteen dogs (8 males, 8 females; mean age±SE = 37.1±7.9 month) were assigned to the 'OC & NO' group; they participated in both OC and NO conditions (see below). This group was made of seven different recognized breeds (2 Yorkshire terriers, 1-1 Beagle, Border collie, Cavalier King Charles spaniel, Golden retriever, Hungarian vizsla, Labrador retriever) and eight mongrels.

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The Baseline Control (BC) group (5 males, 8 females; mean age±SE = 33.2±6.2 month) was made of six different recognized breeds (2 Poodles, 1-1 Beagle, Schipperke, French bulldog, Basset hound, English bulldog) and six mongrels.

Experimental procedures

Warm up trials

Before the experiment dogs participated in a 10-trial warm-up session that served to elicit the dog's interest in the plastic pots shown in the experimental trials. During this the experimenter put a piece of dog chow in a plastic container in full view of the dog and then hid it behind her back. After some seconds she brought the pot and offered it to the dog by holding it up (1 m above ground level) either in her left or right hand (5-5 trials in a counterbalanced order) while making noise by shaking the container. In the first trial the experimenter gave the food to the dog immediately after the dog looked at the container. In the later trials, however, the experimenter gradually increased the dog's looking time toward the container (up to 5 seconds) by increasing the delay interval between showing and shaking the container and giving the food.

Test trials

Subjects were presented with a series of movies in which a human female turned her attention toward one of two identical containers either in an ostensive-communicative (OC) or in a non-ostensive (NO) manner.

The gaze data was collected at 50 Hz by a Tobii X50 Eye Tracker (Stockholm, Sweden). The eye tracker had 0.5-0.7 degree accuracy, 30 x 16 x 20 cm freedom of head movement. The stimuli were presented on a 17-inch LCD monitor positioned behind the eye tracker. The owner made the dog to stand, sit, or lay down in order to get optimal eye gaze data (at a distance of approx. 60 cm). She/he was sitting behind the dog looked down while avoided verbal interactions. The eye gaze recording was preceded by a five-point calibration phase following the infant calibration protocol of Clearview 2.5.1. Same software presented the video clips in the test trials. Dogs participated in the test trials only if contributed to minimum 4 calibration points.

In the Ostensive-Communicative condition (OC) the human actor overtly expressed her communicative intent whereas in the non-ostensive condition (NO) we removed the ostensive signal from the stimulus. Dogs (N = 16) that were exposed to both O and NO conditions received two blocks of 6 trials, where the blocks were composed either of video materials containing ostensive cues (Figure 5.1.2.1 A-B-D), or non-ostensive cues (Figure 5.1.2.1 A-C-D). The blocks were presented in counterbalanced order and the direction of the model's gaze was also counterbalanced (in RLLRLR or LRRLRL order) with at least 1 week break between the two sessions.

Subjects assigned to Baseline Control group (N = 13) received only one block of six trials (Figure 5.1.2.1. A-D, but without attention getter in phase C).

Each trial presented video recordings that started with an introductory phase during which the model that had two pots on each side was facing down in a still position for 2 seconds (Fig. 5.1.2.1.A).

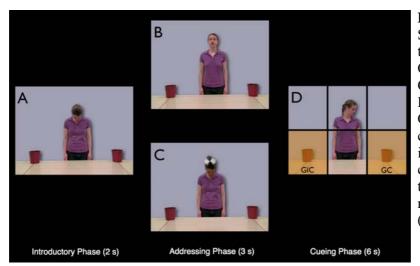


Figure 5.1.2.1 Selected frames from the stimuli in the Ostensive-Communicative (A-B-D) and Non-Ostensive (A-C-D)condi-tions. GC indicates the gazecongruent and GIC the gaze-incongruent regions of interest (ROI).

The second phase was an addressing phase that lasted for 3 s and differed according to the experimental conditions. In the OC (Ostensive-Communicative) condition (Fig. 5.1.2.1.B) the model raised her head, looked straight at the dog and addressed the subject ("Hi dog!") in a high pitch voice. In the NO (Non-Ostensive) condition with her head facing down the model was addressing the dog using low pitch voice ("Hi dog.") while a salient moving image was overlaid on the head (Fig. 5.1.2.1.C). This attention getter was present for 2 s and served to create attentional demand similar to that in the ostensive condition. The verbal signal in the two conditions had similar duration and intensity but differed in pitch.

In the cueing phase (6 s) the model turned her head towards one of the two containers (1 s) and remained motionless (5 s) while showing neutral facial expression (Fig. 5.1.2.1.D).

Data collection and analysis

The screen was divided on the horizontal axis in 3 equal areas: left, middle, and right (see Fig. 5.1.2.1.D). Our statistical analysis was based on the eye gaze collected from the lower half of the lateral (left and right) areas (10.5° x 12° visual angle) that were defined as regions of interest (ROI) during the cueing phase. Trials were accepted as valid only if they provided more than 200 ms eye gaze data from the ROI. This criteria was implemented in order to exclude short transitions of the gaze that just happened to pass the ROIs. While during the cuing phase eye gaze was recorded from the regions of interest in 69% of the trials, taking these criteria into consideration dogs provided 27% valid trials in the OC and 34% in the NO conditions. For dogs participated in BC condition eye gaze was recorded from the target regions of interest in 60% of the trials out of which 35% were valid trials.

Scoring: The gaze following was tested along two measures: cumulative accuracy and first look toward the gaze congruent object. These indexes correspond to those presented by Senju and Csibra (2008). For each of these measures difference scores were calculated. For instance, trials in which dogs looked only to the side congruent with the model's gaze were coded as correct (c), if the dog did not look at the correct side the trial was coded as incorrect (i). When dogs looked at both sides, the trial was classified according to the longer look. Thus, the difference score (d) for the cumulative accuracy was calculated by subtracting the incorrect from the correct

trials and dividing the result by the total number of trials were participant provided valid ROI data [d=(c-i)/(c+i)]. The first look was analyzed in a similar fashion, but instead of the time spent in one or the other ROI only the first gaze record toward these ROIs were considered.

RESULTS

We obtained valid data for analysis from 13 dogs in the OC and 14 dogs in the NO condition, however, only 11 of them provided valid data in each of these conditions (for the validity criteria see Data Analysis). In the addressing phase dogs spent similar amounts of time gazing toward the human actor in the two conditions (mean \pm SE = 1088.8 \pm 181.1 ms in OC and 980.9 \pm 267.8 ms in NO conditions, p > 0.05, ns) and invested a comparable amount of time scanning the region containing the actor's face relative to the whole body: mean \pm SE = .46 \pm 0.09 in the OC condition and .55 \pm 0.10 in the NO condition (paired t-test t(10) = -0.88 p = 0.39) showing that in the addressing phase the human actor evoked the same level of visual attention in both conditions.

Next we analysed whether dogs looked longer at the gaze-congruent area (Fig. 5.1.2.1.D) as compared to the gaze-incongruent area (cumulative accuracy). In accordance with infant eye-tracking studies (e.g. Senju & Csibra 2008), difference scores were calculated for this variable. We found that subjects looked longer to the gaze-congruent area than to the gaze-incongruent area after having seen ostensive addressing (one sample t-test, t(12) = 2.382; p = 0.034). However, this was not the case for the non-ostensive condition in which the difference score did not differ from zero (one-sample t-test, t(13) = -0.756; p = 0.46), indicating no tendency to follow the human's gaze in the absence of communicative addressing (Figure 5.1.2.2).

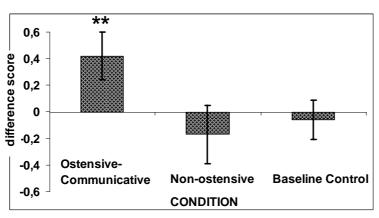


Figure 5.1.2.2.

Difference scores calculated in OC, NO and BC conditions for cumulative accuracy. **p < .05, Error bars represent SE.

This differential sensitivity to human referential gestures is strikingly similar to that of found in a study of 6.5 month-old human infants (Senju & Csibra 2008). A similar analysis on dogs' first look did not reveal any significant bias towards the gaze-congruent area neither in OC nor in the NO conditions (one-sample t-test, t(12) = 1.167; p = .266; t(13) = -.105; p = .91, Figure 5.1.2.3).

Given the absence of a difference in first looks we analyzed also the latencies of first saccades toward the gaze-congruent region of interest. While the comparison did not reach significance, there was a numerical difference in this measure in favour

of the ostensive communicative condition (Mean_{OC} = 1397 ms, SE = 524.01; Mean_{NO} = 1757 ms, SE = 431.39; p>0.05, ns)

A within subject analysis of the difference scores for cumulative looking time in the two experimental conditions was run on the eleven subjects that gave valid data in both conditions. This analysis further confirms the notion that dogs were more likely to follow the model's gaze in a gaze-congruent manner in the OC than in the NO condition (t(10) = 2.49; p = 0.03. Moreover the effect was independent of presentation order: If we analyze the cumulative looking time in an 2x2 ANOVA with order of presentation as between subject and experimental condition as within subject factors gave neither main effect of order (F(1,9) = 2.548; p = 0.14) nor interaction of order with the experimental conditions F(1,9) = 0.867; p = 0.376. Thus we concluded that the order of presentation played no role in our study. However, no difference was found between conditions for the first look (t(10) = -1.21; p = 0.25).

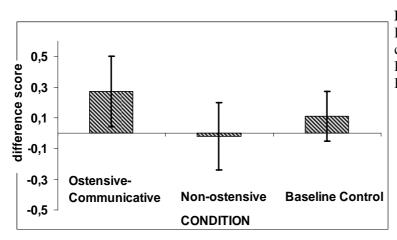


Figure 5.1.2.3.

Difference scores calculated in OC, NO and BC conditions for first look. Error bars represent SE.

We also explored the spatio-temporal pattern of eye movements during cueing phase, investigating how the gaze points move away from the midline of the display and approach the target objects. Gaze points were averaged into 1 s bins and were projected to the X axis of the display (Figure 5.1.2.4). The averaged eye movements showed a greater proximity to the target object only in the ostensive condition.

Thus, we may conclude that dogs' context-dependent responsiveness to human head turning mirrors the specific effect of human ostensive communication on dogs cognitive processing. While the stimuli in the two conditions were equally successful in orienting dogs' attention toward the actor's head in the addressing phase, only the ostensive cues led to gaze following.

However, in order to elicit a comparable saliency of the addressing phases in the two conditions in the NO condition we displayed a moving attention getter on the model's forehead (see Fig. 5.1.2.1C) similar to the infant study (Senju & Csibra 2008). Importantly, however, this raises the possibility that not the absence of ostensive cues but the artificial nature of this stimulus has contributed to the reduced gaze following in the NO condition. To exclude this we measured the gaze following behaviour of 13 additional experimentally naïve dogs in a baseline control condition (BC) in which (i) the human actor turned her head without providing any ostensive cues (eye contact and addressing), (ii) the salient attention getter was removed from the addressing phase and (iii) the verbal addressing was replaced with neutral beep sound of similar duration and intensity in order to keep the auditory marking of this sequence comparable, while attracting the dogs' attention to the screen.

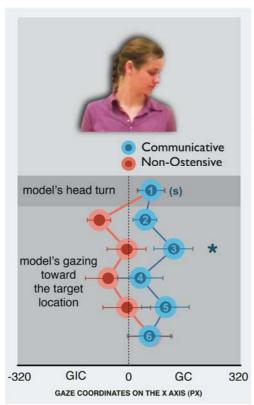


Figure 5.1.2.4.

The temporal dynamic of the eye movements during the cueing phase in OC and NO conditions. The gaze data recorded from the lower half of the screen capture the main trends of eye movements (with gaze coordinates projected to X axis; res. X=1280 pixels) as the mean gaze points move away from the midline of the display towards the gaze congruent (GC) or gaze-incongruent (GIC) region. After the actor's head movement there is a peak that differs significantly from the central axis of the display only during the ostensive condition (*p < .05, Error bars represent SEM, 1° visual angle is approx. 40 pixels, Y axis represents time)

The data showed that gazing toward the region containing the actor's face relative to the whole body in the addressing phase (12 dogs provided sufficient data in the addressing phase of this condition; Mean $\pm SE = 0.60 \pm 0.07$) was comparable to that of found in OC (0.46 ± 0.09) and NO (0.55 ± 0.10) conditions.

However, dogs looked longer toward the body of the protagonist in both OC and NO conditions than in BC (400.2 ± 106.9 ms; 2-sample t-tests: OC vs. BC t(21) = -3.44, p = 0.002; NO vs. BC t(21) = -2.187, p = 0.04). Thus, the combination of visual and audio components of the stimuli available in the addressing phase of OC and NO conditions (direct gaze and infant directed speech or visual grabber and adult directed speech) attracted more attention toward the human actor. Importantly, however, the accuracy indexes calculated for the cueing phase did not capture gaze following in BC (cumulative accuracy: one-sample t-test, t(12) = -.433, p = 0.67; first look: t(12) = 0.695, p = 0.5, see Figures 5.1.2.2 & 5.1.2.3). Furthermore, dogs followed the actor's gaze significantly less in the BC compared to the OC condition (cumulative accuracy, 2-sample t-test, t(24)=-2.107, p=0.045). These data suggest that the lack of gaze following, when there are no ostensive signals, cannot be accounted for by the confounding effect of "artificial" salient attention getter used in the NO condition also providing further support for the significant role of ostensive signals in dogs' gaze response.

DISCUSSION

These results indicate striking similarities between adult pet dogs and preverbal infants as regards their context specific responsiveness to human referential signals. Dogs seem to be receptive to human communication in a manner

that was previously only attributed only to 6-month-old human infants and they can read our intention to communicate in a preverbal, infant-like manner.

This conclusion is supported by the dogs' bias to look longer towards the gaze-congruent area in the cuing phase of the ostensive - but not in the non-ostensive conditions. However, first look measures did not show significant context-specific differences despite the fact that this test variable is usually reported to be one of the strongest indexes to capture human gaze following in presence of ostensive-communicative cues. The discrepancy between the two measures seems to suggest that while being overall sensitive to the ostensive signals, dogs, in contrast to 6.5 month-old infants (Senju & Csibra 2008), might be less responsive to the actual onset of these cues. At an earlier age, even human infants show similar pattern: although 5 month-olds generally prefer to fixate gaze congruent objects, this bias is not reflected in their first gaze shifts (Gredeback et al. 2008). In line with data from a recent study (Williams et al. 2010) one may also argue that dogs are generally less accurate in their first fixations. Finally, it is also possible that our subjects by being allowed to move freely might have produced discontinuous eye gaze recording that introduced more noise in the first look analysis.

5.1.3. STUDY VI. GENERAL DISCUSSION

The results of the present experiments are in line with other observations on dog-human communicative interactions (e.g., Soproni et al. 2001; Call et al. 2003; Kaminski et al. 2009a; Kaminski 2009) showing that dogs are sensitive to the attentional cues of humans and respond sensitively to cues that signal the human's communicative intent (see also STUDY VII).

The interesting aspect of the first experiment is that the dogs' performance shows more advanced features as being restricted only to discriminate between others' states being attentive and inattentive with them. Instead of the "all or none" response relying upon whether the human is facing to the dog or not, dogs displayed different responsiveness when the Instructor oriented to a human partner versus to empty space. This differentiation was significant, despite that the position, the head and body orientation and the verbal and non-verbal cues of the Instructor were the same in both conditions ('Face to human partner' versus 'Look away') and the only difference was that the human Partner was either in or out of the Instructor's focus of attention. These results raise the possibility that dogs do not only engage in gaze following but are capable of visual perspective taking what can be defined as differential responsiveness to humans as a function of the human visual access to some object, subject or critical event (see Emery 2000).

Gaze-following behaviour among humans is an early emerging pervasive response (Butterworth 1991) and is frequently considered as a window into social cognition of different non-human species (Emery 2000). The results of the second experiment suggest that independently from the actual underlying mental mechanisms dogs display analogue functioning in terms of performance to preverbal infants in ostensive-communicative situations. Besides the susceptibility to human ostensive cues, dogs' gaze following behaviour may also be considered as a socially facilitated orientation response with aspects linked to associative understanding of the net utility of the co-orientation with others.

It is also important to note that gaze cues (eye contact, gaze shift) were used in combination with ostensive addressing in the experiments thus the question about

the contribution of individual ostensive cues to dogs' tendency to follow human gaze is still unanswered. Whether these cues act independently or in combination, and whether they can be ranked according to their efficiency in eliciting the communicative understanding of certain social interactions should be a target for further investigations.

The results of this study provide further support for the notion that dogs might have evolved a special, functionally infant-analogue "cognitive mindset", which facilitates the emergence of communicative interaction with people as a result of proper socialization to human environment. Such socially motivated "cue-driven" gaze following displayed by preverbal infants and dogs is a necessary but probably not a sufficient precondition for a deeper understanding of the intentional-communicative nature of referential signals. Altogether, these observations underline the importance of dogs in studying the evolution of social cognitive skills outside the primate line.

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5.2. STUDY VII. THE INFLUENTIAL ROLE OF HUMAN COMMUNICATIVE SIGNALS

Abstract

Many argue that socially provided information is particularly effective in influencing the behaviour of dogs even when the human's action demonstration conveys inefficient or mistaken solution of task. In this study three experiments were designed to test how the social communicative signals affect the dog's behaviour in simple object hide-and-search tasks. In the first experiment we explored whether adult pet dogs (N=35) are able to show inferential reasoning when searching for their toy. Visual cues (sight of the toy or sight of the empty container) and social communicative signals (directional gesture and gaze cues) were combined in six different experimental conditions. Results show that dogs are able to use inferential reasoning by exclusion (i.e. they can find the hidden toy if they have seen where the toy was missing). However, dogs were able to solve a reasoning task only when they could not rely on social-communicative cues and/or could not use any other simple discriminative stimuli (movement of a container) for making decisions.

Results of the second experiment also support the primary importance of social cueing: dogs (N=25) preferred to choose the "socially-marked" container to the remotely moved one when they had no visual information about the location of the toy.

The third experiment aimed to explore how the communicative nature of the demonstration context and the presence of the human demonstrator affect the dogs' (N=60) and 18-month-old infants' (N=57) object-choice behaviour. Beside species-specific differences results showed a significant main effect of the presence or absence of the human communicative signals, and we also found some evidence for the response-modifying effect of the presence of the human demonstrator during both the dogs' and human infants' choice. These findings point to a special form of social influence in both dogs and human infants.

*Based on:

Erdőhegyi Á, Topál J, Virányi Zs, Miklósi Á. (2007). Dogs use inferential reasoning in a two-way choice task — only if they cannot choose on the basis of human-given cues. Animal Behaviour, 74: 725-737.

Kupán K, Miklósi Á, Gergely Gy, Topál J. (2011) Why do dogs (Canis familiaris) select the empty container in an observational learning task? Animal Cognition 14(2): 259-268.

Kupán K, Krekó K, Király I, Gergely Gy, Topál J (submitted manuscript). Imitation versus emulation: communication signals and the demonstrator's presence during re-enactment affect infants' response.

INTRODUCTION

Dogs are evolutionary distant relatives of humans, but have been subjected to very similar ("human-like") adaptational demands during domestication. This could account for the dogs' sophisticated social cognition (see Chapter 2 above for review). Dogs are not only able to make inferences about the communicative meaning of human gestural cues, as in indicating the location of reward, but they seem to understand the communicative cues in complex "triadic" situations where a human alternately interacts either with them or with an other human as well (see e.g. STUDY VI for more details).

On the other hand, some results from understanding means-end connection show that dogs are not able to process sophisticated forms of physical causality (Osthaus et al. 2005) and lend support to the speculations that this "inability" is the indirect consequence of the domestication process (i.e. the selection for physical intelligence was relaxed when dogs were domesticated - Frank 1980). In contrast, others suggest that dogs' poor performance in tasks based on physical causality may be affected by pre-existing biases for social cues. Studies based on object permanence paradigm suggest that the ability to understand causal relationships as well as responsiveness to social cues influence the dogs' performance in simple hideand-search tasks (see STUDY V & STUDY VIII for more details). Others (Szetei et al. 2003; Bräuer et al. 2006) have argued that in particular situations dogs, unlike apes, are more willing to rely on human communicative and behavioural cues to find a reward, than on perceptual cues of the physical world or on causal cue. For example, in two-way choice tasks in which dogs have a possibility to choose one of the possible hiding locations, subjects are biased to select the location mistakenly indicated by the human's ostensive-communicative referential cues even if they had been unambiguously informed about the location of the reward (Szetei et al. 2003). These results are of great importance because in line with other studies (e.g. Hare & Tomasello 2005), they point to the strong impact of human communicative cues on dogs' behaviour and suggest the hypothesis that dogs may also show evidence for infant-like context-dependent "efficiency blindness" in observational learning situations.

One of the striking characteristics of 12- to 24-month-old human infants' social learning is that they are ready to imitate unusual inefficient actions and replicate unnecessary aspects of the observed behaviour even if they themselves could use an obvious, more efficient method for reaching the same goal (Meltzoff 1988). Some studies argued that this "efficiency blindness" reflects the immaturity of causal understanding in infants (Dijksterhuis & Bargh 2001). In addition to causal opacity, another factor that is thought to be important in the emergence of "efficiency blindness" is whether the human demonstrator presents his/her action in an ostensive-communicative-referential manner (see e.g., Bekkering et al. 2000; Carpenter et al. 2002a; Gergely et al. 2002). Converging evidence indicates that infants are prone to show special sensitivity and preference for a basic set of ostensive-communicative and referential signals (such as direct eye contact, being addressed in motherese, gaze-shift etc. - see Csibra & Gergely 2009 for a recent review). Clearly, such early sensitivity to communicative cues may provide a necessary cognitive prerequisite that supports preverbal infants' early emerging competence to engage in different types of social interactions.

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The present experiments aimed to test the hypothesis that dogs show evidence for infant-like context-dependent "efficiency blindness" in two-way object choice tasks.

In the first experiment dogs were provided with direct and indirect visual cues about the location of their favourite toy in order to see whether their choice behaviour could be interpreted in terms of inferential reasoning and/or "blind" responsiveness to social-communicative cues. In the two-way object hide-and-search task the visual cues (i.e. sight of the toy or sight of the empty container) and the attention-getting (social influencing) effect of human manipulation (i.e. touching, moving and looking at the container) were combined independently in the different experimental conditions.

5.2.1. EXPERIMENT VII/1

METHODS

Subjects

Forty two adult pet dogs and their owners were recruited on voluntary basis. The only criterion for selection was that the dogs had to be highly motivated to play with a toy. Three dogs were rejected during the first few trials because they lost their interest in finding and retrieving the ball and an additional four subjects were excluded from the final analyses due to significant side preference (i.e. regardless of the actual place of the toy they approached the same container at least 10 times out of the 12 test trials - binomial test for side bias: p<0.04). The remaining 35 dogs (23 males, 12 females; mean age±SD = 4±2.28 years) included 15 different recognized breeds (7 Parson russell terriers, 5 German shepherds, 2-2 Malinois, Labrador retrievers, Golden retrievers, Rottweilers, German pointers, 1-1 Miniature pinscher, Springer spaniel, Jack russell terrier, Border collie, Pumi, Doberman, Dogo Argentino, Mudi) and five mongrels. All participants were unaware in regards to the hypotheses and goals of the study.

Experimental procedures

The experiments were recorded in a room (5 m x 2.5 m) where two identical containers (turned upside down) were placed 1.5 m apart to hide the toy. Containers were composed of an outer part (a brown plastic flower pot, 22 cm in diameter) and an inner one, a smaller brown plastic flower pot (20 cm in diameter). These were telescoped so, that they could be lifted together or one at a time, by the means of two strings (Figure 5.2.1.1).

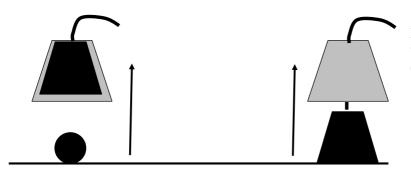


Figure 5.2.1.1. Possible ways of lifting the containers.

Pre-test trials

The owner made the dog to stand at a predetermined point in the room. The experimenter nicknamed the dog and placed the two containers equidistant from the dog (2m). Next she caught the dogs' attention with the toy in her hand and then placed it under one of the containers while she alternated her gaze 3 times between the dog and the baited container. After baiting, she lifted up the baited container to about 40 cm to reveal the ball under the container for 3 seconds, meanwhile she alternated her gaze 3 times between the dog and the manipulated container. Finally, the experimenter replaced the container, took up her initial position, turned her back to the dog and the subject was allowed to choose. If the dog chose the baited container it was allowed to play with the toy for some/a few seconds. The trial was repeated once more, but instead by hiding the toy under the other container. In trials 3 and 4 the same procedure was repeated with the exception that after the baiting the experimenter lifted only the outer part of the container (in the same way as described above). All dogs (but/except those who were excluded due to motivational problems – see Subjects) met the criterion of 3 or 4 correct choices.

Test trials

Each trial consisted of the following three phases:

- (1) Baiting: Having been called and shown the ball, the dog was prevented from witnessing the concealment by a green plastic barrier. The experimenter manipulated the left and then the right container and left the ball under one of them. Then she took up her initial position between the containers and the visual barrier was removed.
- (2) Providing information: The experimenter called the dog and administered one of the six following conditions.

Both

The experimenter showed the content of both containers: first she stepped to the container on her left hand side and lifted it up (both the inner and the outer parts) revealing its content for 3 seconds. In parallel she alternated her gaze 3 times between the dog and the manipulated container. Next she went to the other container on her right and repeated the same procedure.

Baited Only

The experimenter showed only the content of the baited container. She went to the baited container and lifted it up to reveal its content for 3 seconds and alternated her gaze between the dog and the baited container. She did not approach and touch the empty container.

Balanced Baited

The experimenter showed only the content of the baited container (revealing its content for 3 seconds and gaze alternations between the dog and the baited container). She also lifted the outer part of the empty container and made gaze alternations between the dog and the empty container).

Empty Only

The experimenter showed the content of the empty container. She went to the empty container and showed its content accompanied by gaze alternations between the dog and the container but she did not approach and touch the baited container.

Balanced Empty

The experimenter showed only the content of the empty container but lifted also the outer part of the baited container accompanied by gaze alternations between.

Control

The experimenter manipulated both containers while she altered her gaze 3 times between the dog and the hiding places. She did not provide information about the content of the containers because she lifted only their outer parts.

(3) Selecting a container: After these demonstrations the experimenter returned to her starting position, turned her back to the dog and the owner released the dog to allow it to make a choice. If the dog chose the baited container it was allowed to play with the ball for a few seconds.

Each dog received two trials per condition (one left and one right baiting) in a single session (12 trials in all). Order of the conditions and reward positions (left vs. right) was predetermined and semi-random, with the restriction that the ball did not appear more than two times in succession on the same side. The whole session was videotaped and the choice behaviour of the subject was analysed later.

Data collection and analysis

A container was regarded as chosen by the subject if the dog turned it over, or touched it with its paw/muzzle or at least approached it (its paw/muzzle was closer than 10 cm to the container). In order to assess inter-observer agreement, a second person blind to the conditions, scored a randomly selected sample of 20 %. Cohen's kappa value was 1 (100% agreement) showing extremely high level of reliability.

The number of correct choices (0, 1 or 2) was compared between the different testing conditions using nonparametric statistical methods (Friedman ANOVA, Wilcoxon rank sum test and Wilcoxon matched pairs test with false discovery rate correction (FDRbl adjustment, see Benjamini et al. 2001) at the group level.

It is also important to note that subjects could choose between the two possible target places on different decision making processes which can be formulated into "choice-rules". These local rules (Natale et al. 1986) may be effective in helping subjects to recover the target object. In line with this, we also tested the relevance of two possible "choice-rules" for the description of the dogs' performance.

First it is possible that in those conditions, when the experimenter manipulated both containers the sequence of human cueing cause a bias in dogs' choice behaviour (having a stronger aftermath of human cueing in case of the last manipulated container). A second possible "choice-rule" can be formulated as "Go to the container under which the toy was hidden during the previous trial!" It seems reasonable to suppose that the sight of the reward under one of the containers (and getting the toy from under it) could cause the selection of the same container independently of the informing cues in the subsequent trial. Although the willingness to perform such perseverative actions often leads to erroneous choice behaviour

(Watson et al. 2001), in principle, the dog's behaviour can be influenced by this in each condition.

The explanatory value of these rules in each condition for each dog was defined as the number of trials (0, 1 or 2) in which the choice behaviour of the dog was in accordance with the choice resultant from the rule. In line with this scoring subjects can be categorized into three main groups. Their choice behaviour corresponds with the rule in both trials (full correspondence) or only in one of the trials (no preferential use of the rule) or in neither of the trials (ignoring the rule). Using this categorization we have analysed whether subjects relied on any of the choice-rules based upon their decision or showed explicit ignorance of that rule (Wilcoxon signed-ranks tests with FDRbl adjustment).

RESULTS & DISCUSSION

Testing the relevance of the choice-rules for the description of the dogs' performance

Dogs did not follow the "Go to the container which was last manipulated by the experimenter!" rule in any of the conditions. In the Balanced Baited condition only 4 dogs showed full correspondence with the rule, 28 subjects performed no preferential use of the rule and 3 ones ignored it (Wilcoxon signed-ranks test: p > 0.05 ns). The distribution of subjects was similar in the other conditions (Balanced Empty: 9-16-10; Control: 9-16-10; Both: 1-34-0, p > 0.05 ns in each). The "Select the container rewarded previously!" rule was also not preferred in four conditions (Balanced Empty: full correspondence with the rule - 7 dogs, no preferential use of the rule - 22 dogs, ignoring the rule - 7 dogs; Empty Only: 11-18-6; Baited Only: 6-12-17; Control: 10-16-9, p > 0.05, ns in each). Moreover dogs showed significant ignorance of the rule in the two experimental conditions (Both condition: full correspondence with the rule - 3 dogs, no preferential use of the rule - 7 dogs and ignoring the rule - 25 dogs; Balanced Baited: 3-14-18, p < 0.01).

In summary, we found that dogs did not rely on simple choice rules even in the control condition when neither direct (sight of the toy), nor indirect (sight of the empty container) informing cues were given.

Number of correct choices

The performance of the dogs was strongly influenced by the types of the test trials ($chi^2(5, 35) = 110.74$, p < 0.001; Figure 5.2.1.2).

In line with our expectations dogs' performance in non-informing (*Control*) condition was at chance level (T.(35) = 85.5, p = 1, ns). Moreover the number of correct choices was significantly above chance level when dogs were provided direct visual information about the location of the toy (correct responses: *Both* condition – 99.5%; *Baited* condition – 99.5%; *Balanced Baited* condition – 90%, T.(35) = 0, p < 0.001 in each). In these three conditions the number of correct choices was significantly above the performance level shown in the *Control* trials (*Both* condition: T.(35) = 9.5, p < 0.01, *Baited Only* condition: T.(35) = 0, p < 0.01; *Balanced Baited* condition: T.(35) = 8.5, p < 0.01; *Balanced Empty condition*: T.(35) = -26.0, p < 0.05).

Regarding those two conditions when dogs were exposed to indirect visual information (i.e. they were shown the content of only the empty container) there were significant performance differences. Dogs performed significantly better than chance when they were shown the content of only the empty container, although both

had been manipulated by the experimenter (*Balanced Empty*: T.(35) = 8.5, p < 0.001). In contrast, when the experimenter had manipulated only the empty container showing its content (*Empty* condition), the dogs chose the baited one below chance level ($T_+(35) = 10.5$, p < 0.001) and their performance was significantly lower compared to that shown in the *Control* condition $T_+(35) = 45.0$, p < 0.01).

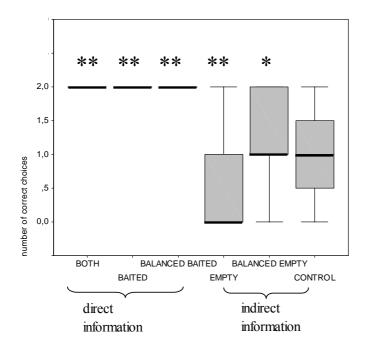


Figure 5.2.1.2.

The number of correct choices in the different types of test trials in the "social" task (median, quartiles and extremes). Significant differences from control are indicated by *: p < 0.05, **: p < 0.01 (N=35, Wilcoxon matched pairs tests with FDRbl adjustment).

These results show that, not surprisingly, dogs were able to solve the search-for-the-toy task when they had been informed about the location of the toy by direct visual cues (sight of the toy). However in those conditions in which a human gave indirect visual cues (sight of the empty container) the dogs' performance was strongly influenced by the accompanying cues. When human manipulation was unbalanced (i.e. only the non-rewarded container was moved and marked by the human socially) dogs showed clear preference for the obviously empty container suggesting that these perceptual cues could supersede the reasoning abilities in dogs. In contrast, when dogs could observe communicative cues (looking at and touching) and movement for both target places in a balanced fashion, they were able to choose the rewarded container even if only the content of the empty one had been shown. This suggests that dogs can still infer the location of their toy relying on inference by exclusion.

Unconscious cueing of the human participants or smell of the reward did not influence the dogs' choice behaviour as their performance was at chance in the control condition. Results suggest that dogs are able to perform simple inferential reasoning, but in fact they are often prevented from showing this competence by pre-existing biases for such salient cues as movement of the container and social marking of some hiding locations. However, in this experiment these two types of perceptual information could not be separated from each other and the relative importance of "social marking" versus moving of the container could not be established.

5.2.2. EXPERIMENT VII/2

Results above have shown that human manipulation (social-communicative component: approach, gaze alternations, directional gestures toward the container) and/or the movements of the containers (non-social attention-capturing component) make that location attractive for the dogs despite the fact that the manipulated container is shown to be empty. Therefore the next experiment was designed to answer the following questions:

Does human manipulation of the empty container override the effect of direct visual information (sight of the reward in the non-manipulated container)?

Which component, the social-communicative or the non-social discriminative ones, can be regarded as the more important factor in the dogs' choice? Using a novel apparatus (see Figure 5.2.2.1) we could separate the following factors from one another upon cueing: (I) social cues (approach, touching, gaze-alternation), (II) the movements of the container, and (III) showing the content of the container.

METHODS

Subjects

Twenty-six adult pet dogs (15 males, 11 females; mean age±SD = 3.2±1.92 years) participated in this experiment and the only criterion for selection was that the dogs had to be highly motivated to play with a toy. None of them participated in the first and the second experiments. One female dog was excluded after the first few trials due to motivation problems. Thus the experimental group consisted of 25 dogs of eight different breeds (4 Border collies, 2-2 Parson russell terriers, Malinois, 1-1 Jagd terrier, Airedale terrier, Golden retriever, Groenendael, Jack russell terrier) and 12 mongrels. All participants were unaware in regards to the hypotheses and goals of the study.

Experimental procedures

Experimental observations were recorded in the same room as in Experiment VII/1. In this case however, the experimenter could show the content of the boxes without any direct manipulation by hand (control was achieved remotely by a thin nylon string – see Figure 5.2.2.1 and Figure 5.2.2.2).

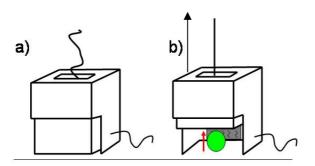


Figure 5.2.2.1.

The container in "closed" (a) and in "open" position (b).

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The two boxes were attached to a wooden frame with two pairs of strings which were used for moving the boxes either vertically or horizontally. The upper side of the frame was covered by a black screen so that the experimenter could lift the front side of the boxes or could move the boxes horizontally by using the strings in an unobtrusive manner. Each box could be positioned either at the point labelled P1 (close to the frame position) or at P2 (distant position). At the beginning of the trials, the dog was held by its owner at a distance of 2 m from the experimenter whilst the experimenter was standing behind the screen equidistant from the boxes and was facing the dog.

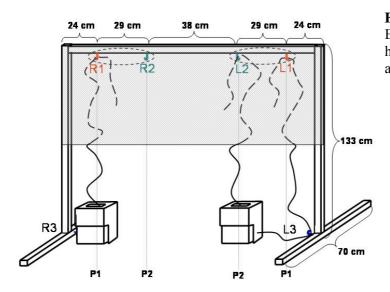


Figure 5.2.2.2. Experimental apparatus. Six hooks are labelled as R1-3 and L1-3.

Pre-test trials

The procedure for the pre-test trials was basically the same as in Experiment VII/1. except that the experimenter made the ball visible by lifting the inner box by the string. In the four consecutive trials, all dogs except for one individual, met the criteria of at least 3 correct choices

Test trials

Test trials consisted of the same steps as in Experiment VII/1 (Baiting; Providing information; Selecting a container) and the basic procedure were identical to that described above. After baiting, the experimenter called the dog by its name and administered one of the following conditions.

String / Baited Only

Boxes were placed near to the frame (P1 -see Figure 5.2.2.2). The experimenter stood behind the screen seemingly motionless and elevated the inner part of the baited box to reveal the ball by using the string (R1 or L1). She was wearing black sunglasses in order to avoid any unconscious cueing. After 3 seconds the inner box was lowered and the dog was allowed to make a choice.

String / Both

Arrangement of the boxes and the way of informing the dog was the same as in *String / Baited Only* condition, however, the experimenter showed the contents of both containers by using the strings (R1 and L1).

Human / Baited Only

Boxes were placed near to the frame (P1), the screen was removed and the experimenter did not wear the dark sunglasses. The way of informing was identical to the *Baited Only* trial in Experiment VII/1. The experimenter stepped to the baited box and lifted its inner part revealing the content of the box for 3 seconds. In parallel she alternated her gaze 3 times between the dog and the manipulated container. Then she returned to her starting position, turned her back to the dog and the owner released the dog to make its' choice.

Human / Both

The position of the boxes and the method of informing was the same as in *Human / Baited Only* condition with the exception that the experimenter showed the contents of both containers.

Visual cue vs. Human-given cues

The two boxes were close to the frame. One after the other, the experimenter showed the content of the baited box by using the string (R1 or L1) similarly as in *String/Baited Only* condition, and manipulated the empty box as well without showing its content: the experimenter put her palm on its top and alternated her gaze 3 times between the dog and the manipulated container. Finally, she returned to her starting position (behind the screen) and put her sunglasses on.

Visual cues vs. Box-Movement

The rewarded box was placed close to the frame (P1) while the empty box was at a distant position (P2). The experimenter remained behind the screen throughout the trial wearing dark sunglasses. She showed the content of the baited box by the string (R1 or L1 - as described above) and pulled the empty container from P2 to P1 position by the help of the horizontal string (R3 or L3).

Human-given cues vs Box-Movement

The experimenter showed the content of neither the baited nor the empty box. One of the boxes was placed close to the frame (P1) while the other one was in distant position (P2). The experimenter put her palm on the top of the first box and alternated her gaze between the dog and this box three times. Then she returned to her starting position (behind the screen) and put her sunglasses on. The other box was remotely moved from P2 to P1 position using the horizontal string (R3 or L3). In one of these two trials the human-manipulated box was baited, in the other trial the string-moved box contained the toy.

Control

Both hiding places were located close to the frame (P1). The experimenter did not provide information about the content of the boxes: she stood motionless wearing the sunglasses behind the screen for 10 seconds and then the dog was allowed to make a choice.

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Each dog received two trials with each condition in a single session (16 trials in all). Similarly to Experiment VII/1, all conditions were presented in semi-random order and the position of the reward (left vs. right) was also randomly determined with the restriction that the ball did not appear more than two times in succession on the same side.

Data collection and analysis

The number of correct choices was recorded and compared to chance level (Wilcoxon signed rank tests) and Wilcoxon matched pairs tests with FDRbl adjustment used to make pair-wise comparisons between conditions.

RESULTS & DISCUSSION

Performance in conditions involving direct visual information

Dogs were significantly above the 50% chance performance in those conditions when they had received direct visual information about the content of either the baited box only or both the baited and the empty ones (String / Baited Only: T.(25) = 0, p < 0.001; String / Both: T.(25) = 0, p < 0.001; Human / Baited Only: T.(25) = 0, p < 0.001; Human / Both: T.(25) = 0, p < 0.001). Moreover dogs performed above chance level also in the two testing conditions when the direct view of the reward and the social cues or the movement of a box were presented on conflicting sides (Visual cues vs. Human-given cues: T.(25) = 0, p < 0.001; Visual cues vs. Box-movement: T.(25) = 0, p < 0.001). Accordingly in all of these conditions (where direct visual information regarding the whereabouts of the toy was given) the dogs' performance was significantly better than in the Control trials (Wilcoxon matched pairs tests with FDRbl adjustment: p < 0.01 in each case). It seems evident that when the bait was directly seen under the baited box, neither the social cues (human manipulation) nor the movement of the empty box were sufficient to distract the dogs' choice.

Performance in non-informing conditions

The number of correct choices were at chance level in the *Control* condition where no cues were given at all $(T_+(25) = 13.5, p = 0.547, ns)$. In this condition, dogs chose from among the boxes randomly and they did not even show any side bias (testing was based on the number of dogs choosing the right side against the hypothetical median of 1 and did not show significant difference; $T_+(25) = T_-(25) = 68, p = 1, ns$).

In the *Human-given cues vs. Box-movement* condition where dogs were also not informed about the location of the toy, subjects showed preference for the human-manipulated box, that is, dogs chose the human-manipulated box more often than the moving box $(T_{-}(25) = 50, p = 0.039)$. 14 out of the 25 dogs repeatedly chose the human-manipulated box whereas only 5 of them chose the moving box twice and 6 of them chose the human manipulated box and the moving box once each during the two trials.

In agreement with our observations in the first experiment, these results underline the dominant role of the direct visual information (sight of the toy) when dogs are allowed to see where the toy is and to select one of the two containers after it. Furthermore, our results suggest that social-communicative cues (approach,

touching, gaze-alternation) can be considered as the more important factor for the dogs' choice in comparison with nonsocial-discriminative stimulus (movement of the container). When dogs had no direct information about the location of the toy but could witness the seemingly self-propelled moving away of one of the boxes and human communication cues (tapping, looking at) towards the other one, subjects showed significant preference for the human-manipulated target place. That is, more individuals chose repeatedly the "socially-marked" container than the remotely moved one

The results from these two experiments support the notion that dogs' reasoning ability is suppressed by a prevailing bias to attend movements and human ostensive-communicative manipulation and this behaviour can be regarded as functionally analogous to that shown by human infants. Ostensive-communicative and referential cues can guide the infants' attention and influence their inferences and interpretations about the action demonstration so that they will be more willing to re-enact unusual and less efficient actions (see STUDY VIII for more details). Moreover, many argue that in some of the cognitive tasks, human infants show similar patterns of success and error suggesting that children's competence is often hidden by bias which is a simple heuristic whose usefulness and prevalence declines with age (Mitchell 1996).

5.2.3. EXPERIMENT VII/3

Reviewing the recent literature, it is unclear, however, how the two potentially interacting factors, the ostensive-communicative signals of the demonstration context and the presence of the human instructor during the choice contribute to the emergence of the aforementioned efficiency blindness in the dog as compared to human infants. Therefore, in this study, we investigated how the different combinations of these two factors affect the behaviour of dogs and 18-month-old infants in a two-way choice observational learning task. In the demonstration phase subjects could see how a tennis ball can be retrieved from under an opaque container by the manipulation of a distant and obviously empty (transparent) one. Importantly, the situation was conflicting as subjects could either rely on the observed action (selecting the human-manipulated empty container) or emulate the goal by performing a more efficient alternative solution (selecting the baited container).

METHODS

Subjects

Dogs: 87 adult pet dogs and their owners were recruited from various dog training schools. Participation in the tests was voluntary and the only criterion for selection was that the dogs had to be highly motivated to play with a toy. Seven dogs were excluded from the final analyses due to technical reasons (inaccurate demonstration — 4 dogs; problem with the recording — 1 dog; the owner did not act in line with instructions — 2 dogs). There were twenty dogs that were unwilling to participate in the test (totally lost interest in the task and did not make any choice). The sixty dogs of 24 different breeds and 18 mongrels (31 males and 29 females;

mean age $\pm SD = 3.8\pm 2.4$ years, range: 1–14 years) that were included in the final analyses were participated randomly in five experimental groups (see Table 5.2.3.1).

Infants: 81 toddlers (47 boys, 34 girls, mean age = 18 months, range: 17.1–18.9 months) with their parents participated. Twenty four infants were excluded from the analysis because of different reasons: parental interference — 8 infants; failed demonstration — 4 infants; technical problems with the recording — 1 infant; did not make any choice (refused to participate) — 11 infants. Each subject was tested only once.

Experimental procedures

Dogs were tested either at the Department of Ethology, Eötvös Loránd University, Budapest (N=53) or at the Department for Behaviour, Neurobiology and Cognition, Vienna University (N=23). Infants were observed in a room at the Institute of Psychological Research, Hung. Acad. Sci. The same experimental setup and apparatus were used in each case.

A transparent and an opaque plastic container of similar shape and size (16 cm high and 16 cm in diameter) were placed 0.6 m apart. Both were turned upside down and placed on a black platform (20 x 20 x 6 cm). The white opaque container was used to hide the target object (a tennis ball). The platform was slightly aslope so that the tennis ball rolled down if the baited container was elevated. The two containers were connected by the means of a string, which was led through 2 pulleys that were fixed to the ceiling. An orange curtain covered the pulleys, and this was also used to prevent the dogs from witnessing some of the manipulations with the containers (see below). This apparatus makes the demonstrator possible to lift the opaque (baited) container by means of moving the empty transparent one horizontally (see Figure 5.2.3.1).

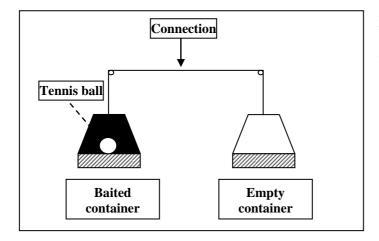


Figure 5.2.3.1. Schematic representation of the experimental apparatus

The procedure included two phases. First, the human repeatedly (three times) demonstrated a less efficient solution of the task (i.e. she obtained the target object by means of manipulating the empty container - demonstration phase) and finally the subject was allowed to explore the experimental set up (Test trial).

<u>Demonstration phase</u>

The dog was led by the owner to a predetermined point, at a distance of 3 m from the apparatus, and held it there by its collar. The parent was asked to sit down

on a chair facing the containers (at 3 m distance) and was asked to hold the infant on his/her lap. The demonstrator got the ball and placed it under the opaque container, while the curtain prevented the dog/infant from witnessing the baiting procedure. Subjects witnessed the demonstrations in one of the following contexts (see Table 5.2.3.1):

Communicative demonstration (Com)

The demonstrator (a 25-year-old woman) who was standing between the two containers pulled back the curtains and looked at the dog. She addressed the subject ("Subject's Name]! + Watch!"), and when the dog/infant looked at her face, she bent her upper body and touched the two containers simultaneously. Then, she took an upright position and addressed the subject again ("Look at this!"). At the moment, the demonstrator could make eye contact with the dog/infant she crouched grasping the transparent empty container by both hands and placing it to the ground ahead of the platform (Figure 5.2.3.2a). Thereupon, the baited container elevated and the tennis ball rolled out towards the dog/infant. The demonstrator turned her head towards the ball shifting her gaze conspicuously from the subject to the ball. Finally, she picked the ball up and dropped it to the ground two times, but she did not give it to the subject. She closed the curtain and replaced the ball under the opaque container.

Non-communicative demonstration (NonCom)

The procedure was identical to that described in the communicative demonstration condition, except for that the demonstrator performed the actions without ostensive—communicative signals (Figure 5.2.3.2b). That is, she did not look at the dog/infant and never addressed it. During the whole procedure, the demonstrator was mumbling a short poem. This was to attract the subject's attention to the demonstration non-communicatively, without giving any direct instruction to the dog/infant. The position of the baited container (left or right hand side) was counterbalanced between subjects in each group.

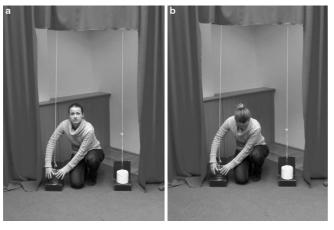


Figure 5.2.3.2.

Photo illustration of the a Communicative demonstration (Com) and b Non-Communicative demonstration (NonCom)

Immediately after the third demonstration, the demonstrator closed the curtain and placed the ball under the opaque container. Then, she pulled back the curtains again and either left the room (*Demonstrator absent* condition) or remained there (*Demonstrator present* condition). In the latter case, she was standing motionless at a predetermined point (on the left side of the dog/infant). Once the demonstrator left or took her predetermined position, the owner (mother) released the dog (infant) and

encouraged it (saying "You can go!" It's yours!") to explore and manipulate the apparatus. The trial was terminated after 20 s (for dogs) and 90 s (for infants). During the test trial, the demonstrator did not talk to and did not look at the subject.

The whole session was videotaped by two cameras (one facing the subject and one facing the experimental apparatus), and the behaviour of subjects was analysed later.

Group	Demonstration phase:	Test phase:	Dogs: males & females (mean age ±SD)	Infants boys & girls
Com- D/present	Communicative demonstration	Demonstrator present	11 & 6 (4.3±3.5)	7 & 8
Com- D/absent	demonstration	Demonstrator absent	8 & 7 (4.2±1.9)	7 & 7
NonCom- D/present	Non-communicative	Demonstrator present	6 & 8 (2.5±1.9)	6 & 8
NonCom- D/absent			6 & 8 (4.5±3.1)	7 & 7

Table 5.2.3.1. Summary of the experimental conditions and subjects

<u>Com-D/present Group</u>: 2 Border collies, 1-1 Airdale terier, Appenzeller, Golden retriever, Malenois, Russian terrier, Kelpie, Parsons russel terrier, Sheltie and 7 mongrels

<u>Com-D/absent Group</u>: 4 Border collies, 1-1 Basset hound, Groenendael, Malenois, Pincher, Mudi, Hovawarth, Labrador retriever, German shepherd and 3 mongrels

NonCom-D/present Group: 2 Golden retrievers, 1-1 Briard, Border collie, Dachshund, German shepherd, Hungarian vizsla, Labrador retriever, Transylvanian hound and 5 mongrels

NonCom-D/absent Group: 2-2 Border collies, Golden retrievers, 1-1 Briard, Malenois, Springer spaniel, Labrador retriever, Staffordshire terier, Foxterrier, English bulldog and 3 mongrels

Data collection and analysis

A container was regarded as chosen if the dog turned it over or touched it with its paw/muzzle or at least approached it (its paw/muzzle was closer than 5 cm to the container), and if the infant turned it over or touched it with his/her hand. There were two infants who clearly selected a container without touching it (approached and pointed at it). In these cases this response was coded as choice behaviour. To assess inter-observer agreement, a second person blind to the demonstration condition scored a randomly selected sample of 63% (dogs) 90% (infants). Cohen's kappa values were 0.904 (dogs) and 0.927 (infants) showing a high level of reliability.

We recorded the subjects' 'First choice' (i.e. whether the dogs/infants inspected first the baited or the empty container) and we also coded the subjects' 'Shift between the locations' (i.e. whether subjects proceeded to the baited container after the empty one had been visited). The effects of demonstration context (communicative vs. non-communicative), and the presence of demonstrator during the test trial on the dogs' first choices was analysed by Generalized Linear Model for binary data (SPSS, version 17). For the analysis of the dogs' and infants' first choice, we also employed binomial tests to see whether there was significant bias towards the empty or baited location within the groups. Due to multiple comparisons levels of

significance (p) were corrected (FDRbh adjustment, see Benjamini & Yekutieli 2001).

RESULTS & DISCUSSION

The GLM analysis of the subjects' first choice as a function of both independent variables (presence or absence of the human's communicative action; presence or absence of the demonstrator during choice) showed significant effect of the demonstration context for both dogs ($Com\ vs.\ NonCom$; $chi^2(1) = 7.585$, p = 0.006) and human infants ($chi^2(1) = 9.599$, p = 0.002). In contrast, the presence of the demonstrator was not significant ($D/present\ vs.\ D/absent$; dogs: $chi^2(1) = 1.163$, p = 0.281, infants: $chi^2(1) = 0.964$, p = 0.326). The interaction of the two factors proved to be significant for infants ($chi^2(1) = 6.225$, p = 0.013) but not for dogs ($chi^2(1) = 1.163$, p = 0.281).

A group by group analysis of the firstly selected container showed that the presence or absence of the demonstrator during choice had no influence on dogs' first choice in the non-communicative demonstration contexts (subjects preferred to choose the baited container in both *NonCom-D/present* and *NonCom-D/absent* conditions; binomial test, p < 0.01 for both). However, after having watched a communicative demonstration, dogs showed the same selection bias only when the demonstrator was absent (binomial test, p < 0.05) but not when she was present (binomial test, p = 0.332). In the case of human infants this analysis provides a somewhat different picture: Infants showed a significant tendency to choose the empty container in the in the communicative demonstration contexts (*Com-D/present*: p < 0.05; *Com-D/absent*: p < 0.01) and a significant tendency to approach and inspect the baited container first in the *NonCom-D/absent* condition (p < 0.05) (Figure 5.2.3.3).

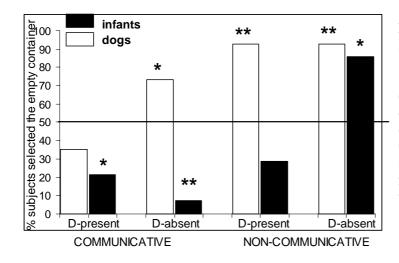


Figure 5.2.3.3. Percentage of dogs infants approaching and inspecting the baited container first in the different demonstration contexts. **p < 0.01; *p < 0.05; in comparison with the success rate expected by random search (binomial tests).

Shift between the locations

During the test trial, subjects had a possibility to approach and inspect both containers, or they could select only one of these. Based on these possibilities dogs and infants were categorized in one of the three response categories (i.e. "empty only", "baited only" and "empty then baited"). Table 5.2.2.3 indicates that infants predominantly gave 'empty only' response in the two communicative demonstration

contexts (*Com-D/present & Com-D/absent*) as well as when after having seen non-communicative demonstration the human demonstrator remained present (*NonCom-D/present*). Infants choose an emulative solution (i.e. selecting the baited container) only when they saw non-communicative demonstration and the human was not present in the test phase.

	Container inspected by the subject						
	Empty Only	Empty then Baited	Baited Only	Empty Only	Empty then Baited	Baited Only	
Groups		DOGS			INFANTS		
Com-D/present	35.3%	29.4%	35.3%	66.7%	13.3%	20%	
Com-D/absent	6.7%	20%	73.3%	78.6%	14.3%	7.1%	
NonCom-	0%	7.2%	92.8%	42.9%	28.6%	28.6%	
D/present							
NonCom- D/absent	0%	7.2%	92.8%	7.1%	7.1%	85.7%	

Table 5.2.3.2. Proportion of dogs and infants inspecting 'only the empty'; 'only the baited'; or 'first the empty and then the baited' containers during the test trials.

Dogs, however, selected the baited container in all but one condition. Only those dogs who were tested in the presence of the demonstrator after having witnessed ostensive–communicative demonstrations (*Com-D/present* group) showed infant-like ("imitative") response pattern. In this condition the majority of those dogs who inspected first the empty container (6 out of 11 individuals) seemingly ignored the toy object as they *did not proceed* to the baited container after the empty one had been visited. In the other three conditions there were only 6 dogs (out of 43 individuals) that approached first the empty container and almost all of them (5) proceeded to the baited container within few seconds.

Dogs' and infants' performance in the non-communicative & demonstrator absent condition clearly indicates that the unusual and causally opaque demonstrations (i.e. remote manipulation of the baited container) in general cannot distract the subjects' attention from the goal and cannot inhibit the subjects from approaching the baited container directly. It seems however, that the accompanying ostensive-communicative signals and the presence of the human demonstrator during the test trial affect subjects' choice behaviour.

Infants' predominantly "imitative" responses in the communicative demonstration contexts are in line with earlier findings (Király et al. 2004; Nielsen 2006; McGuigan et al. 2007) and this is also congruent with the natural pedagogy account (Csibra & Gergely 2009). That is the context-dependent performance of 18-month-olds may stem from selective encoding of the social learning situation in which the presence of the demonstrator has an important modulatory role on interpretation of the task. The ostensive-communicative demonstration can be interpreted as teaching manifestation that triggers a less efficient "imitative" response, whereas the non-communicative demonstration focuses infants' attention to the goal that can be best achieved by emulation.

Although in general dogs preferred the simpler, evident solution (direct approach) over the less efficient demonstrated one, there was a combination of the situational factors that led to a reduced tendency of goal directedness. Namely, when

human manipulated the empty container expressing her overt communicative intention towards the dog and she was still present during the testing phase (*Com-D/present*), subjects did not show significant bias to the baited container.

One possible explanation of dogs' infant-like efficiency blindness in the strongest ostensive-communicative condition is based on a motivational account. Recent evidence suggests that in social learning situations ostensive-communicative cues may trigger higher levels of arousal and activity in dogs (Range et al. 2009a). Thus, one may assume that the change in the dogs' search pattern lies in the differential motivational effect of the different demonstration conditions. That is, dogs were better motivated to participate in the task (they were more willing to approach and inspect the apparatus as a whole) in the communicative demonstration conditions and this, incidentally, led to a higher probability of visiting the empty container. This account, however, is not supported by our observations showing that dogs made their choice shortly after having released (within 3–5 s on average) in each condition, and there were only three dogs out of the 57 (2 in *Com-D/present* and 1 in *NonCom-D/present* groups) that did not make their first choice within 10 s. This suggests that although dogs were similarly motivated to participate in the task, there could be specific differences in their decision-making processes across contexts.

Another explanation can be raised on the basis of the dogs' attention and memory processes. Recently, it has been shown that attention is an important variable when testing dogs in social situations (Range et al. 2009b). In line with this, one may suppose that signals expressing the demonstrator's communicative intent focused the dog's attention to the steps of demonstration and therefore enhanced the capacity of the dog to encode the human's actions during the observation and display more effective recall during choice (see also Pongrácz et al. 2004). Moreover, the presence of the human demonstrator in the testing phase probably acted as a "reminder cue", which facilitated recalling the demonstration. It follows from these that the presence of the human demonstrator in the test phase and the communicative signals as a part of the demonstration could have had an independent (additive) effect leading to a decrease in goal-directed search behaviour (selecting the baited container). Importantly, our results do not seem to support this account as we could find only marginal effect of the human's presence during the test phase on the dogs' choice behaviour.

Third, we can offer a social communicative account, for the findings we found. In this experiment, human demonstration might have two possible roles: acted as triggering and facilitating either a preference for obtaining the desired object in the most efficient way or rather to act in line with the human demonstration. In the former case, the demonstration could be perceived as not having communicative flavour and moving of the empty container simply informed the dog about the goal of the task ("there is a ball under the opaque container"). Results show that dogs in the non-communicative demonstration contexts mainly utilized this kind of emulative meaning of the observed demonstrations and they preferred the effective. species-specific solution (approaching the baited container directly). However, the human's demonstration could also be perceived as communicative manifestation that acted as not only making the subject to recognize the location of the reward but manifesting a specific behaviour. This raises the possibility that the demonstration of this causally opaque, inefficient action was regarded as a communicative manifestation of an "episodic imperative" by the human ("Go to the empty container!").

5.2.4. STUDY VII. GENERAL DISCUSSION

As a summary of the above experimental observations we can conclude that those conditions in which demonstrations were accompanied by the human's communicative signals, especially if the human demonstrator remained present during test trials, dogs showed some tendency of using the human referential cues to specify the spatial location where the act was required to be performed, and as a consequence, they selected the baited container less frequently in comparison with other demonstration contexts.

The first experiment of this study provides one of the few experimental evidences for inferential reasoning in dogs (see also Kaminski et al. 2004). Interestingly however, our results suggest that this ability is often masked by their bias for cues of human communication. Namely, human cues are much more important for the dogs than the sight of the empty container and based the results of the second experiment it seems that human-given cues can even be more important than salient discriminative stimuli, such as the moving of the hiding places.

Dogs' tendency to carry out a counterproductive response in object choice situations if one location is misleadingly indicated by the human communicative cues fits well with some earlier observations (Szetei et al. 2003; Prato-Previde et al. 2008). Our findings are also in line with the social-dog, causal-ape hypothesis (Bräuer et al. 2006) suggesting that dogs, unlike chimpanzees, would rather use the human communicative (pointing, looking at) and behavioural cues (trying to open a box or trying to reach something) while they fail to use the causal cues (e.g. the presence or absence of the noise or the smell of the food) to find the hidden reward in observational learning situations. Accordingly it can be speculated that the restricted manifestation of dogs' reasoning abilities is not due to the effect of domestication in the reduction of problem solving abilities (Frank 1980) but it is being masked by bias in following social cues. This would be in line with our dependency argument (see Topál et al. 1997). The notion that dogs prefer to use the human demonstrator as a "social tool" to reproduce the desired result is gained further support from the finding that only a few (2-6) dogs obtained the reward on their own in the different demonstration conditions of the third experiment as if they were waiting for the human's help in spite of the fact that retrieving an object from under an opaque container is motorically not a demanding task for a dog.

In addition to providing further support for the importance of the social communicative signals in observational learning situations, the results of the present study raise the possibility that like in infants (see also Király 2009), the presence of the human demonstrator also plays some behaviour modulating and constraining role in observational learning situations when it comes to learning about causally opaque and less efficient (compared to what comes natural to the dog) action demonstrations. In certain situations, dogs' behaviour is probably driven by a motivation to satisfy ostensively signalled human imperatives in the "here-and-now" (see also STUDY VIII) and the ostensively communicated human action demonstrations can be functionally interpreted as imperatives by dogs with the function of performing the observed action in the presence of (and "for") the human demonstrator.

In agreement with the studies showing specific sensitivity to human's communicative signals in dogs (e.g., Kaminski et al. 2009b; Riedel et al. 2008), our results suggest that for the dog, the function of human demonstration is not (only) transferring knowledge but disposing behaviour actions. Supposedly, this form of

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social influence has been evolved to evade conflicts in the group and to co-operate in common actions without any deeper insight into the knowledge content of other's mind. Nevertheless, future studies are needed in order to reveal, whether the influential effect of communicative signals of the demonstration context on dogs' choice actually reflected their willingness to follow a specific order or communicative cueing and other contextual factors simply distracted them from the more effective, emulative solution.

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5.3. STUDY VIII. SUSCEPTIBILITY TO HUMAN COMMUNICATIVE SIGNALS AS AN EXPLANATORY FRAMEWORK OF THE PIAGETIAN Anot-B ERROR.*

Abstract

Having repeatedly retrieved an object from a location, human infants tend to search the same place even when they observe the object being hidden at another location. This perseverative error is usually explained by infants' inability to inhibit a previously rewarded search response or to recall the new location. In the first experiment we show that the tendency to commit this error is substantially reduced when the object is hidden in front of 10-month-old infants without the experimenter using the communicative cues that normally accompany object hiding in this task. This result clearly shows that communicative cues from the experimenter contribute to the emergence of this perseverative search error.

In a second experiment we replicate these results with adult pet dogs, who also commit more search errors in ostensive-communicative than in non-communicative or non-social hiding contexts.

In the next experiment we test whether simple learning processes and/or confounding effects of procedural factors play an important role in dogs' perseverative error. The results of this experiment support the hypothesis that the dogs' A-not-B error may reflect a special sensitivity to human communicative cues.

A further comparative investigation indicates that human-reared wolves do not show dog-like context-dependent differences of search errors. This finding supports the notion that shared sensitivity to human communicative signals stems from convergent social evolution of the Homo and the Canis genera.

However, the results of the fifth experiment show some species-specific differences suggesting that communicative signals serve different functions for dogs and infants. In sum, these findings provide an alternative theoretical perspective on the nature of infants' and dogs' perseverative search errors.

*Based on:

Topál J., Gergely Gy., Miklósi Á., Erdőhegyi Á., Csibra G. (2008). Infants' perseverative search errors are induced by pragmatic misinterpretation. Science, 321 (5897), 1831-1834.

Topál, J., Gergely, Gy., Erdőhegyi, Á., Csibra, G., Miklósi, Á. (2010). Differential sensitivity to human communication in dogs, wolves and human infants. Science, 325 (5945), 1269-1272.

Topál, J., Miklósi, Á., Sümegi, Zs., Kis A. (2010). Response to comments on "Differential sensitivity to human communication in dogs, wolves and human infants." Science, 329 142d 1624 doi:10.1126.

Kis, A., Topál, J., Gácsi, M., Range, F., Huber, L., Miklósi, Á., Virányi, Zs. (in press). Does the A-not-B error in adult pet dogs indicate sensitivity to human communication? Animal Cognition

INTRODUCTION

Subjects' abilities for understanding the physical world are often tested in hide-and-search tasks, including the standard A-not-B task (Piaget 1954). A classic phenomenon of this experimental paradigm is the perseverative search error (sometimes called the A-not-B error), a well-known and robust mistake that infants close to one year of age and some other nonhuman species normally commit (see Gomez 1995 for a review).

In the standard A-not-B task, a demonstrator repeatedly places an object under one (A) of two opaque containers ('A' and 'B') in full view of the subject. After each hiding event, the subject is allowed to retrieve the object. This is followed by test trials where the demonstrator places the object under container 'B' and allows the subject to search for it. Despite just having seen the object being hidden at the new location, infants between 8 and 12 months of age frequently look for it under container 'A' where it had been previously hidden.

During the past decades, a wide range of explanations have been proposed to account for this response bias and the phenomenon continues to be of theoretical interest for researchers of infant cognitive development (see e.g., Wellmann et al. 1987 for a review). The A-not-B error is usually ascribed to a deficit in inhibitory control over a previously rewarded motor response (Diamond 1985), or to constraints on short-term memory (Bjork & Cummings 1984), or to an attentional bias to the location where the previously observed manual responses have been directed (Ruffman & Langman 2002). Others suggest that observing repeated hiding events at location 'A' leads to automatic motor simulation (covert imitation) of the action through the activation of the mirror neuron system (Longo & Berthental 2006).

In contrast to the focus of such accounts on infants' repeated responses directed at container A, we have examined the perseverative error from a different perspective by exploring the potential role of the communicative demonstration context of the task. The A-not-B task normally involves face-to-face interaction, in which object hiding is accompanied by the demonstrator's ostensive and referential signals (such as eye-contact, infant-directed speech, addressing the baby by name, pointing at and/or looking back-and-forth between the hiding location and the infant, see Csibra & Gergely 2006).

Convergent findings indicate that human infants pay special attention to various non-verbal communicative signals directed at them (such as eye contact, gaze-shifts, and pointing – Gergely et al. 2007; Senju & Csibra 2008; Yoon et al. 2008). Recent evidence suggests that signals conveying manifestation of intention to communicate induce a learning attitude (a receptive 'pedagogical learning stance' - Csibra & Gergely 2009) in infants, which enables them to acquire knowledge from observation of adults' demonstrations. That is, ostensive-referential communicative signals can play an interpretation-modulating role leading to selective encoding of different aspects of action demonstrations in social learning tasks (e.g., Brugger et al. 2007; Nielsen 2006).

In line with these findings the hiding events in the standard A-not-B task can be interpreted not only as indicating episodic information about the referent's current location ("the target object is now under container A"), but as communicating information about some generalizable property of the referent kind (e.g., "this type of object is usually found in container A") or as "imperatives" with the function of performing the observed action (e.g., "produce search behaviour at location A").

5.3.1. EXPERIMENT VIII/1

In the first experiment we hypothesized that in the A-not-B paradigm the human infant's built-in interpretive bias of generalizability may result in a pragmatic misinterpretation of the object hiding actions as potential teaching demonstrations. As a result, after having witnessed the ostensive-communicative hiding actions during the 'A' trials, the infant would tend to commit the perseverative search error during 'B' trials because they infer and learn some generalizable information such as "this kind of object is to be found in container A" or "we keep toys in container A". To test this hypothesis, we examined infants' object search behaviour in the A-not-B task in conditions varying the presence or absence of the social-communicative context of the hiding events. We predicted that in a non-communicative action observation condition, which lacks ostensive signals but provides experience with repeated motor search responses directed at container 'A', the perseverative search error should be significantly reduced.

METHODS

Subjects

Forty-two 10-month-old infants participated in the experiment (22 boys, 20 girls; mean age±SD = 308±16.3 days). They were assigned to the ostensive-communicative (N = 14, 9 boys, 5 girls; mean age 309.6 days), non-communicative (N = 14, 8 boys, 6 girls; mean age 308 days) and non-social (N = 14, 5 boys, 9 girls; mean age 306.1 days) hiding contexts so that the distribution of age and gender would not differ by condition. Six additional infants failed to pass the reaching criterion in the 'A' trial phase (see Procedure) or totally lost interest in the task by the end of the 'A' trials, and 4 infants were excluded from the final sample because of parental interference. Infants were recruited from a database at the Research Institute for Psychology, Hungarian Academy of Sciences, and were given a small gift for participating. The parents of all participants gave informed consent.

Experimental procedures

The experiments took place in a room $(4 \times 4 \text{ m})$ at the Institute for Psychological Research. Only the mother, the infant and the experimenter were present during the procedure, which was video-taped for later evaluation. The object hiding tasks were presented on a rectangular $(60 \times 120 \text{ cm})$ table with a cardboard sheet $(80 \times 20 \text{ cm})$ on it. Two identical brown plastic flower pots (15 cm high, 12 cm diameter) served as hiding containers. In most trials, we used a yellow toy babyphone $(5 \times 8 \text{ cm size})$ as the target object, which could be clanked by pushing a button. However, if the infant lost his/her interest in this toy, we continued the task with other attractive objects of similar size.

Two identical containers were placed upside down on the cardboard sheet 40 cm apart. The infant sat on the mother's lap at one side of the table, equidistant (70 cm) from the two containers. The task included two phases: hiding the target object repeatedly under the container on the infant's right-hand side ('A' trials), and then

hiding it under the other container ('B' trials). Before each trial, the mother was instructed to close her eyes. Infants witnessed the hiding events in one of the three conditions: *Ostensive-Communicative*, *Non-Communicative*, and *Non-Social* contexts (Figure 5.3.1.1 a-c).

Ostensive-Communicative (OC) context

The experimenter, sitting opposite to the infant, placed the target object at the starting position, just right (from the infant's point of view) of container A. She attracted the infant's attention to it verbally ("[Name]! + Look") and by making a conspicuous noise with the target object (ringing the baby-phone, or tapping the toy on the table). Then she started to move the object slowly towards container 'A', lifted the container with her other hand, and lowered it onto the toy. At this point she established eye-contact with the infant and addressed him/her in motherese ("Look!") while looking back-and-forth twice between the object and the baby. During this procedure the experimenter made sure that the infant was following the object. If it was necessary (e.g., if the baby looked away), she interrupted the hiding action and started the trial again.

After lowering the container, the experimenter waited for 4 s before she pushed the cardboard sheet with the containers towards the infant. When the containers arrived within the infant's reach, the mother was allowed to open her eyes but was not allowed to interact with the infant. We considered the infant's first touch of either container as his/her choice. If the infant selected the correct (baited) container, the mother gave him/her the toy for a short play. During this time, the experimenter withdrew the cardboard sheet and the containers to their original position. The mother then took the object away from her infant and replaced the toy at the starting point. If, however, the container touched by the baby was the empty one, its content was shown to her/him and then the experimenter withdrew the cardboard sheet with the containers. If the infant did not touch any of the containers within 20 seconds the trial was terminated. In such cases (i.e. when selecting the empty container or nothing) the experimenter took the toy out of the baited container in full view of the infant and placed it at the starting position.

The experimenter presented 4 consecutive 'A' trials. If the subject made more than one incorrect search response (touched first the 'B' container or did not touch any of the containers within 20 seconds), they were presented with two additional 'A' trials. Two infants received these additional trials in the OC context. The infants who failed to select the baited container more than twice during the 'A' trials (6 in total) were excluded from the analysis.

The 'B' trials followed immediately the 'A' trials. In these trials, the experimenter attracted infants' attention to the toy at the starting position as in the 'A' trials, and then started to move it towards container 'A'. However, in contrast to the 'A' trials, she did not use any communicative signals (eye-contact, gaze-shifts, or infant-directed speech) when lifting container 'A'. The target object was moved uninterrupted across the table towards container 'B', passing under container 'A', after which the container was lowered back onto the cardboard. When the target object was halfway between the two containers, the experimenter made it emit a conspicuous noise (by making it ring or tapping the table with it) to attract the infant's attention to the object. Then the experimenter lifted container 'B', moved the object under it, and lowered the container onto the toy. Note that throughout the object-hiding procedure in the 'B' trials the experimenter focused on the target object

and never looked at the infant. After lowering container 'B' onto the target object, the experimenter withdrew her hands and surreptitiously dropped a pen from her lap onto the floor. The infant could not see the pen, but heard the noise it made when landing on the floor. This served to orient the infant's attention away from the container. Post-test inspection of the videotapes revealed that only in 2 out of the 42 'B' trials did the infant keep focusing on container 'B' during the delay period. After the 4-s delay, the experimenter slid the cardboard with the containers toward the infant and waited for a search response as in the 'A' trials.

Non-Communicative (NC) context

Infants in this group witnessed the same object manipulations as above, but the experimenter performed the actions without ostensive-communicative signals. That is, she did not make eye contact or gaze shifts between the toy and the infant, and never talked to the infant. She attracted the infants' attention to the target object only by the sound effects described above (ringing the phone, etc.), and broke the infants' fixation with the containers by dropping a pen. (In 41 out of the 42 'B' trials, this manipulation worked in the NC group.) In addition, the experimenter sat at the table turning 90° away from the infant, and observed what the infant was doing in a window that reflected the setting as a mirror. This way, the experimenter could adjust her manipulations according to the infants' attention. When hiding the toy under container 'A' or 'B', the experimenter turned towards the table, but she did not raise her eyes to the infant. Six infants in this group received 2 additional 'A' trials because they searched under the in the 'B' container more than once during the first 4 'A' trials.

Non-Social (NS) context

The experimental procedure was the same as in the NC context, except that the infant could not see the experimenter, who acted from behind a curtain. The curtain was mounted on a wooden frame on the table between her and the containers. The experimenter slid the target object under the curtain so that most of it was visible to the child. She operated the containers by fine nylon cords, and pushed forward and withdrew the containers by the cardboard sheet from behind the curtain. The experimenter's hands were never visible to the infant throughout the hiding procedure. When the infant did not retrieve the object, the experimenter withdrew the containers by the cardboard sheet, lifted the baited container by the nylon cord and removed the object in full view of the infant. As in the NC context, she monitored the procedure and infants' behaviour by the image reflected in the window. In response to the dropping pen, infants looked away from container 'B' in 39 out of the 42 'B' trials in this group. Because they made more than one mistake during the first 4 'A' trials, 3 infants received 2 additional 'A' trials in this group.

Data collection and analysis

From the video recordings, we coded, as infants' choice, the first container that they touched. If there was no such response for 20 seconds, or if the infant touched both containers simultaneously, it was judged as "no choice". Two observers scored infants' responses independently in the 'B' trials. The inter-observer reliability was excellent (Cohen's kappa = 0.97). We also measured response latency

in each trial, i.e., the time elapsed between the moment when containers arrived within the infant's reach and the first response.

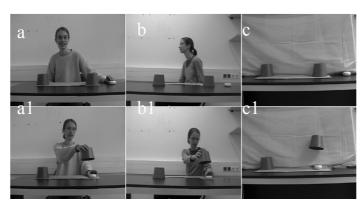


Figure 5.3.1.1.

Experimental arrangement in the three hiding contexts. In the ostensive-communicative context (OC) (Figure a-a1), the demonstrator established eye contact with the baby, smiling at and addressing him/her in infant-directed speech (saying 'Hello baby, look here!'). Then she repeatedly hid a toy object under container 'A' while shif-

-ting her eye-gaze back-and-forth between the infant and the container to direct and share the infant's attention towards the object hiding action. In the non-communicative context (NC) (Figure b-b1), the demonstrator's face and torso was oriented 90 degrees away from the infant and she never looked at or communicated with the infant in any way while hiding the object. In the non-social context (NS) (Figure c-c1), the demonstrator acted from behind a curtain and only the object's movements were visible to the infant.

RESULTS

We analyzed the proportion of correct responses in both the 'A' and the 'B' trials, and the number of infants who committed the A-not-B error (searched more than once at location 'A' in the 'B' trials) as a function of the hiding context. We found that the magnitude of the A-not-B error was considerably smaller in the non-communicative and non-social conditions than in the traditional ostensive-communicative context (Figure 5.3.1.2).

A two-way ANOVA on the proportion of correct responses with phase ('A' vs. 'B' trials) and hiding context (OC, NC, NS) as factors showed more correct responses in the 'A' than in the 'B' trials (F(1,39) = 49.376, p < 0.0001) and a significant interaction between these factors (F(2,39) = 8.041, p = 0.001). This interaction was due to the fact that the change of the proportion of correct searches from the 'A' to the 'B' trials differed across contexts. While in the OC context the initial success rate of 0.88 in the 'A' trials dropped to 0.19 in the 'B' trials (t(13) = 8.917, p < 0.0001), the drop was much smaller in the NC context (0.80 to 0.52, t(13) = 2.536, p = 0.025) and was not statistically significant in the NS context (0.78 to 0.59, t(13) = 1.96, p = 0.072). In addition, while the infants were similarly successful during the 'A' trials in all contexts (F(2,39) = 1.525, p = 0.23), their search performance differed significantly across contexts in the 'B' trials (F(2,39) = 6.660, p = 0.005). In this latter case, post-hoc pair-wise comparisons (Tukey-Cramer test) showed that infants searched the least correctly in the OC context (OC vs. NO: p < 0.05, OC vs. NS: p < 0.01).

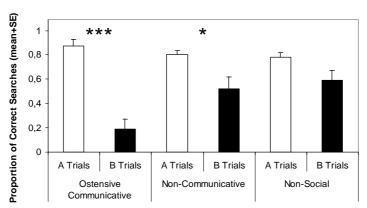


Figure 5.3.1.2. Proportion of correct searches (mean+SE) in 'A' and 'B' trials as a function of the hiding context. The 10-month-old infants received four 'A' trials, followed by three 'B' trials. ***: p < 0.0001; *: p < 0.05

Comparison of the number of infants committing the A-not-B error (Table 5.3.1.1) indicated a significant difference between demonstration conditions (chi²(2) = 8.265, p = 0.016). After having witnessed ostensive-communicative hiding demonstrations during the 'A' trials, 86 % of the infants displayed the perseverative error during the 'B' trials. In contrast, the majority of infants in the other two contexts (NC: 57% and NS: 64%) did not show a perseverative response pattern.

Context	0 or 1 error	2 or 3 errors
Ostensive-Communicative	2	12
Non-Communicative	8	6
Non-Social	9	5

Table 5.3.1.1. Number of infants in the three different hiding contexts (14 in each group) committing at most one or more search errors (searching at location 'A') in the three 'B' trials.

Performance in the 1st 'B' trials

Restricting the measure of the search performance to the first 'B' trials (i.e., to the first trial after location change) revealed similar results to those reported in the main text. In the OC condition, 12 out of 14 infants reached for the 'A' container in the first 'B' trial. This proportion is significantly different from chance by binomial test (p = 0.013). In contrast, infants in the other two contexts were equally likely to search the 'A' or 'B' containers in the first 'B' trials (NO: 8 of 14, NS: 6 of 14 reached for the 'A' container).

Reaching latency

Infants touched one of the containers on average within 5 seconds in both the 'A' and 'B' trials (Table 5.3.1.2). Comparisons between the three contexts showed similar latencies in both the 'A' (F(2,39) = 1.349, p = 0.271) and the 'B' trials (F(2,39) = 0.92, p = 0.407). Within group analyses also failed to show significant differences in the mean reaching latency between 'A' and 'B' trials (OC: t(13) = 1.1, p = 0.285; NC: t(13) = 0.59, p = 0.566; NS: t(13) = -0.2, p = 0.845).

	Context			
	Ostensive-	Non-Communicative	Non-Social	
	Communicative			
'A' trials	4.1±4.0	2.4 ± 2.0	3.1±1.9	
'B' trials	2.8 ± 2.6	1.9 ± 2.2	3.3 ± 3.2	

Table 5.3.1.2. Mean latency (s) \pm SD of first reaching as a function of experimental context and phase.

These results strongly support the notion that infants' tendency to commit Anot-B error reflect "predilection for learning general rules" rather than originating from motor, inhibitory, or memory limitations. It is important to mention, however, that an alternative account can also be offered in terms of attentional processes. This suggest that the role of communication signals was simply to increase infants' attention, that is, infants may have paid *more attention* to the experimenter's activities when they were accompanied by communicative signals. In order to test the plausibility of this explanation we have analyzed infants' gaze direction in the ostensive-communicative (OC) and non-communicative (NC) conditions. A frame-by-frame encoding of infants' gaze direction in the 'A' trials from the point when the toy started to move to the point of total occlusion under the container provided almost exactly the same total looking time (averaged across infants) to the object in the communicative (mean \pm SD = 9.24 \pm 2.24 s) as in the non-communicative (mean \pm SD = 9.31 \pm 2.57 s) context. These data confirm that "just attracting attention" is not sufficient to facilitate perseverative search errors.

DISCUSSION

The robust association between the ostensive-communicative context of the hiding actions and the perseverative search error supports the "natural pedagogy" hypothesis Csibra & Gergely 2009), according to which the perseverative error is in large part due to a pragmatic misinterpretation of the experimenter's hiding actions as constituting a communicative "teaching" demonstration rather than being just a hide-and-search interactive game. This account proposes that ostensive-referential signals have a special interpretation-modulating role in early social learning. The action demonstrations of the A-not-B paradigm can be interpreted either as a hideand-search game presenting the infant episodic (here and now) information about the whereabouts of the object (correct interpretation), or as a kind of teaching session that conveys generalizable information about properties of the objects (toys or containers) for the infant to learn (incorrect interpretation). We propose that it is this latter kind of - mistaken - interpretation established during the ostensively demonstrated 'A' trials that remains dominant during the 'B' trials leading to the erroneous perseverative search responses. We should note however, that this conclusion does not invalidate the contribution of other cognitive factors to the Anot-B error identified by earlier studies (e.g., Diamond 1990; Diamond et al. 1989; Keen et al. 2003).

5.3.2. EXPERIMENT VIII/2

However, humans are not the only species that show special sensitivity to

human ostensive-referential signals. Recent results indicate a functionally similar sensitivity and preference in dogs for certain nonverbal cues of human ostensive and referential communication (see also STUDIES VI & VII). Unlike great apes (Hermann et al. 2007), dogs exhibit some understanding of human referential intentions expressed in communicative gestures, such as pointing, as shown by their success in solving the so-called object choice tasks (Miklósi & Soproni 2006; Riedel et al. 2008).

To investigate the functional nature of dogs' sensitivity to ostensive-referential cues in a comparative manner, here we utilized the same A-not-B object search paradigm that had been used in Experiment VIII/1 above. We tested whether communicative signals would have a significant effect on dogs' tendency to perseverate in a search task.

METHODS

Subjects

Dogs for the experiments were recruited from the Family Dog Research Database at the Department of Ethology, Eötvös University. In order to be selected for this study the subject had to be motivated to retrieve a toy object naïve to the task, and older than a year. At the time of testing all owners were unaware of the hypotheses and goals of the study.

Thirty six adult pet dogs of different recognized breeds (5 Border collies, 3-3 Belgian tervuerens, Labrador retrievers, 2-2 Hungarian vizslas, Mudis, Springer spaniels, Malenois, 1-1 Australian shepherd, Bulldog, Cavalier, Cocker spaniel, German shepherd, Irish setter, Jack russel terrier, Jagd terrier, Parson russel terrier, Miniature pincher, Rottweiler, Siberian husky, Welsh terrier) and three mongrels participated in this experiment (16 males 20 females; mean age ±SD = 3.9±2.3 years). They were assigned to the *Ostensive-Communicative* (N = 12; 5 males and 7 females; 9 different breeds; mean age 5.1 years), *Non-Communicative* (N = 12; 5 males and 7 females; 9 different breeds; mean age 4 years) and *Non-Social* (N = 12, 6-6 males and females; 10 different breeds; mean age 2.9 years) hiding contexts quasi-randomly so that the distribution of age and gender did not differ by condition.

Experimental procedures

The experiment took place in a room (5.0 m x 3.0 m) where two opaque plastic screens (30 cm wide x 40 cm high 10 cm deep) were placed 0.6 m apart to hide the toy. The owner made the dog to stand facing the screens equidistant (2m) from the two hiding locations. He/she was standing behind the dog and restricted the animal's movements by holding its collar. The target object was either a tennis ball or a rubber squeezable toy of similar size depending on the preference of the dog and its motivation to grab it. The target object was placed on the floor 0.6 m from the left screen (from the dog's point of view) in the line of the screens (Figure 5.3.2.1). Only the owner, the dog and the experimenter were present during the procedure, which was video-taped for later evaluation.

The experimental procedure included pretraining and test trials. Test trials consisted of 4 'A' trials when the hiding occurred at the location on the subject's left side (behind screen 'A'), and 3 'B' trials during which the hiding occurred at the other location (screen 'B').

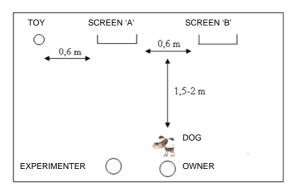


Figure 5.3.2.1.Schematic representation of the experimental arrangement.

Pretraining trials

The purpose of the pretraining trials was to familiarize the subject with the retrieval task and with the experimental situation. By gently touching its body, the owner got the dog to stand orienting towards the screens (at 2 m distance), and the experimenter, who was standing in between the screens, showed the toy object to the dog. Then she placed it under full view behind one of the screens, and the dog was released and allowed to search for the toy. This procedure was repeated once for each screen. These trials were repeated once if the subject did not approach the baited screen. Only those animals were included in the next phase that did not show any sign of distress and were motivated to fetch the toy from behind both screens.

Test trials

The task had the same structure in all experimental conditions: Hiding the target object four times behind the screen 'A' ('A' trials) and then hiding the object three times behind the other screen ('B' trials). Each dog participated in one of the following three conditions:

In the Ostensive-Communicative (OC) condition, the hider attracted the dog's attention by ostensive addressing signals ("[dog's name] + Watch!"). Then she picked a rubber ball from the floor while establishing eye-contact and addressing the dog ("Watch!"), and walked to screen 'A' with the toy in her hand being constantly visible to the dog. As she placed the ball behind screen 'A', she displayed gaze shifts looking back and forth between the hiding location and the dog. Finally, the experimenter returned to the dog walking behind screen 'B'. Having arrived close to the dog, the experimenter presented her empty hands to the dog for a few-second inspection. Then she stood behind the subject and the owner, who held the dog's collar up till now when she released the dog prompting it verbally ("You may go!"), but without using any additional instructions or gestures to encourage searching ('A' trials).

'B' trials were similar to the 'A' trials, except that now the experimenter did not leave the toy behind screen 'A'. Having left screen 'A', the experimenter showed up the toy object in her hand conspicuously, and established eye contact with the dog. Then she placed the toy behind screen 'B' by bending her upper body.

In the Non-Communicative (NC) condition, the experimenter performed the

same object-hiding manipulations as in the OC condition with her back turned towards the dog. Thus, neither eye contact nor facial cues were displayed while the experimenter held the object in her hand clearly visibly to the subject. In addition, she did not talk to the dog but attracted the dogs' attention by clapping her hand (at the start of each trial) and making a conspicuous noise with the toy before placing it behind the screen in both 'A' and 'B' trials.

In the *Non-Social* (NS) condition, dogs observed the toy moving without any visible human manipulation. The experimenter remained still next to the dog while another experimenter, who was invisible to the dog, made the ball move behind the screens by pulling a transparent string (invisible to the dog) to which it was attached. No communicative signals were displayed towards the dogs.

Data collection and analysis

The screen first inspected (i.e. touched and/or watched behind it) by the subject was considered as chosen. Dogs received score 1 or 0 depending on whether they chose the baited or the empty location in the trial. If a subject inspected the hiding locations in a way that it could have equal visual access to the content of both (e.g., it passed along the midline in between the screens) the trial was judged as ambiguous choice and subject received score 0.5. After choosing the baited screen, the subject was allowed to play with the toy for a few seconds, and was praised verbally. If the subject visited the empty screen first, it did not get the toy, the owner ordered it to come back and praised it verbally in the same manner as in the case of "correct choice". Then the experimenter placed the object to the starting point, while the dog was prevented from witnessing this manipulation by placing a large (1 x 1 m) green plastic opaque occluder between the dog and the screens. Inter-observer agreements for subjects' choice behaviour were assessed by means of parallel coding of the 80% of the total trials by two observers. Inter-observer reliability was excellent (Cohen's kappa = 0.85).

RESULTS & DISCUSSION

Dogs fetched the object reliably during the 'A' trials in all three conditions (mean percentage of correct choices: 94% in OC; 98% in NC and NS groups). However, during the 'B' trials, we found striking context-dependent differences in the number of dogs committing the A-not-B error (Generalized Linear Model for binary data, $chi^2 = 26.857$, p < 0.0001, Table 5.3.2.1.).

Number of Perseverative Errors				
Condition	Zero	One	Two	Three
Ostensive-Communicative	0	3	3	6
Non-Communicative	5	3	1	3
Non-Social	8	2	2	0

Table 5.3.2.1. Number of dogs in the three different hiding contexts (12 in each group) performing different numbers of search errors (searching at location 'A') in the three 'B' trials.

After having witnessed the hiding demonstrations during the 'A' trials, all dogs in the OC group selected the empty (A) location at least once (A-not-B error), whilst in the other two hiding contexts many subjects (NC: 41.7% NS: 66.7%) did not display the perseverative search error at all (Fischer's exact tests, OC vs. NC p = 0.0373, OC vs. NS p = 0.0013).

A one-way ANOVA on the response scores also showed highly significant differences (F(2,33) = 10.436, p < 0.001). Post-hoc pair-wise comparisons (Tukey-Cramer test) revealed that dogs in the OC condition searched at the baited screen (B) less often than those in the NC condition (p < 0.05) or in the NS condition (p < 0.001). In addition, dogs in the OC condition displayed a search bias towards the empty (A) screen, as they performed well below the success rate expected by random search (t(11) = 3.576, p = 0.004). In contrast, dogs in the NS condition were significantly more successful than chance during the 'B' trials (t(11) = 3.867 p = 0.003) (Figure 5.3.2.2).

These results clearly indicate that, similarly to human infants (see Experiment VIII/1 above), the communicative context induced in dogs a tendency to perseveratively (and erroneously) search for a hidden object at a previously repeatedly baited location (A) even when they observed the object being hidden at a different location (B). This error, however, has been eliminated when the hiding events were not accompanied by communicative signals. Thus it seems that, contrary to previous accounts (Watson et al. 2001), the perseverative search tendency found in dogs cannot be explained as stemming from an inability to locate hidden objects. Moreover, if the social-communicative signals simply had a distracting effect, one would expect random search and not an explicit bias to the empty location (A), which we found in the OC condition. Therefore we propose that search error in dogs and infants may be indicative of their shared social competence that involves preparedness for learning from others through communication.

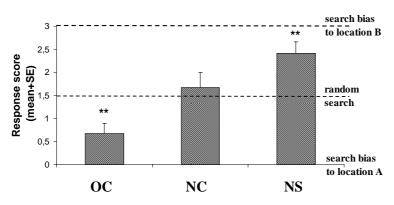


Figure 5.3.2.2. Scores of correct responses +SE) in the 'B' trials as a of the function hiding context. The dogs (n=12 for condition) received four 'A' trials, followed by B' three trials. OC condition: the human experimenter repeatedly hid a toy object behind screen 'A' and then behind screen 'B' using ostensive-

communicative signals. NC condition: the experimenter performed the same object-hiding manipulations as in the OC but without ostensive-communicative signals. NS condition: The experimenter remained still next to the dog while the object moved behind the screens without any perceivable human manipulation. **: p < .01 in comparison with success rate expected by random search (0.5×3) 'B' trials).

5.3.3. EXPERIMENT VIII/3

Although it is possible that the context-specific errors made by dogs are caused by similar processes as in infants, simpler learning processes or confounding effects of procedural factors can also account for them. In the next experiment, therefore, we address questions related to hypotheses derived from these alternative accounts.

First, independently from the presence of ostensive-communicative cues, the A-not-B error made by dogs can be caused by the fact that during the 'B' hidings, instead of moving on a straight route, the reward is following a roller-coaster trajectory visiting first location 'A' and only then 'B' (see the procedure of Experiment VIII/2 above). This 'sham-baiting' of the 'A' location in the 'B' trials raises the possibility of strong proactive interference increasing the chance that dogs mix up earlier memory traces of the toy being at location 'A' in the 'A' trials with the more recent input of seeing the toy disappearing at location 'B' in the 'B' trials (Fiset 2010). In order to examine whether the attentional demands of this distractive component of the hiding contribute to the dogs' A-not-B error, we tested whether dogs show a reduced tendency to commit the error if location 'A' is not sham-baited in the 'B' trials ('Alleviated B trials' group – see below in Procedure).

Second, as often suggested in infant studies (e.g. Smith et al. 1999), dogs may commit the error in the 'B' trials because they cannot inhibit the prepotent motor behaviour of searching at location 'A' after doing so several times in the 'A' trials. This hypothesis has not yet been tested in dogs. Thus, in a group of dogs, by modifying the ostensive-communicative (OC) hiding procedure of Experiment VIII/2, we examined whether dogs commit fewer errors if they only watch repeated hidings at location 'A' but are not allowed to search there actively ('Only watching during A trials' group)

Third, it is also possible, that the dogs' A-not-B error stems from the "unbalanced" cuing procedure of the social communicative hiding context and does not indicate unique susceptibility to human communication. That is, whilst in the 'B' trials of the non-communicative (NC) context the experimenter used sound stimuli (by squeezing the toy) both before the toy is hidden behind 'A' and 'B' screens subjects were not provided communicative signals adjacent to the 'B' barrier in the OC condition of Experiment VIII/2. This means that the cuing procedure in the OC condition was more unbalanced because the experimenter did not recall the dogs' attention using any conspicuous noise. We therefore observed the search behaviour of dogs in two novel versions of the OC condition of Experiment VIII/2 ('Com^A-Sound^B' & 'Sound^A-Sound^B' groups – see in Procedure)

METHODS

Subjects

Adult pet dogs (N = 106) of different breeds participated in the study (51 males, 43 females; mean age \pm SD = 4.3 \pm 2.4 years). They were assigned to four different groups quasi-randomly so that the distribution of age and gender did not differ across groups. Fourteen dogs were excluded from the experiment either because they failed to fulfil the criteria in the pre-training trials (N = 9), lost interest in the task in midstream (N = 3) or their owners disobeyed the experimenter's instructions (N = 2).

Experimental procedures

The experimental arrangement, behavioural coding and analysis and the steps of the experimental procedure was the same as described in Experiment VIII/2 (see above). However, depending on the group they were assigned to, subjects witnessed one of four different hiding procedures.

'Only watching during A trials' group (Watch-A, N = 26)

(13 males, 13 females; mean age±SD: 4.1±2.5 years; 4 Australian shepherds, 3 Border collies, 2 zwergpudels, 1-1 Flat retriever, Labrador retriever, Rottveiler, Newfoundland, Malenois, Königspudel, Pincher, Malteser and 9 mongrels)

In this group we aimed to investigate the effect of the motor response in the 'A' trials. Therefore the procedure used in this condition was the same as in the OC condition (see Experiment VIII/2 above) except that subjects were not allowed to search for the toy in the 'A' trials. Instead, after having arrived at the location close to the dog, the experimenter pulled out the toy remotely from behind screen 'A' by a string fixed to the ball. After the toy had been retrieved in this way, the dog was allowed to play with it for a few seconds without leaving its place. In the 'B' trials, subjects were allowed to search for the toy as in the OC condition.

'Alleviated B trials' group (Allev-B, N = 34)

(19 males, 17 females; mean age±SD: 4.4±2.4 years; 7 Border collies, 1-1 Australian shepherds, Cairn terier, Dalmatian, Foxterier, German shepherd, Golden retriever, Hungarian vizsla, Labrador retriever, Malenois, Munsterlander, Pyrenees, Rottveiler, Weimaraner, Zwergpinscher and 15 mongrels)

This group was designed to control for the 'sham baiting' that occurred in the 'B' trials of the OC condition (in Experiment VIII/2). In this condition, dogs witnessed the same hiding procedure as dogs in OC, with the only exception that during the 'B' trials the experimenter did not 'sham bait' the toy behind screen 'A'. She walked up to screen 'B' following the same track as in the OC, while holding the toy visibly in her hand at the height of her eyes and looking continuously at the dog.

$$\underline{\text{`Com}^A\text{-Sound}^B\text{'}}$$
 (N = 16)

(7 males, 9 females; mean age±SD: 4.2±2.7 years; 1-1 Border collie, Cocker spaniel, Dachshund, Dogo canario, German pointer, German shepherd, Golden retriever, Groenendale, Havanese, Sharpei, Schipperke, Parson russels terrier and 4 mongrels)

In this condition, similarly to the procedure of OC condition in Experiment VIII/2, we used strong communicative cues adjacent to 'A' barrier in both 'A' and 'B' trials (Com^A). However, in this case we used conspicuous non-social sound signals before hiding the object behind 'B' barrier in the 'B' trials (Sound^B). That is in the 'B' trials, before hiding the toy at 'B', the experimenter recalled the dog's attention by squeezing the toy (with her back turned toward the dog).

'Sound^A-Sound^B',
$$(N = 16)$$

(9 males, 7 females; mean age±SD: 4.1±2.6 years; 2-2 Golden retrievers, Labrador retrievers, Hungarian greyhounds, Hungarian vizslas, 1-1 Dachshund, Poodle, Rhodesian ridgeback, Lurcher, Bologense, Tibetian terrier and 2 mongrels)

In this condition dogs participated in the very same procedure as in the Com^A-Sound^B except for that during the 'B' trials experimenter used the same non-social cuing at location 'A' and 'B'.

RESULTS & DISCUSSION

Dogs fetched the object reliably from behind screen 'A' during the 'A' trials in each groups; the proportions of correct searches were between 94.8-98.5%. During the 'B' trials, however, subjects displayed perseverative search bias to the empty (A) location performing well below the success rate expected by random search both in the 'Watch-A' (24% correct, one-sample t-test: t(25) = -3.635, p = 0.0013) and 'Allev-B' (25% correct, t(33) = -4.082, p = 0.001) groups (Figure 5.3.3.1). Choice behaviour in the first 'B' trials (Binomial test, test proportion: 0.5) showed a similar below chance performance in the 'Allev-B' (p = 0.001) and 'Watch-A' (p = 0.001) conditions.

The high tendency of the subjects to commit the A-not-B error in the attentionally less demanding condition ('Allev-B') indicates that sham baiting at location A, a potentially important factor for proactive interference, is of little importance in dogs' search bias towards the empty 'A' location. Dogs also showed a perseverative response pattern in 'B' trials if they did not have the possibility to actively search in the preceding 'A' trials. Based on these results, we can conclude that neither an inability to inhibit previously rewarded motor response nor insufficiencies in their working memory and/or attention skills can explain dogs' perseverative response bias.

Further results show that in contrast to the non-social sound stimuli by which the experimenter recalled the dogs' attention before hiding the toy behind screen 'B' and thus made the 'B' location salient (Com^A -Sound^B condition) dogs tended to commit the A-not-B error (i.e. they performed below the success rate expected by random search: 29.3% correct, t(15) = -2.248, p = 0.04). If, however, after social-communicative 'A' trials the experimenter enhanced both 'A' and 'B' locations equally (Sound^A-Sound^B condition), dogs selected randomly (correct choices: 50%, t(15) = 0.0 p = 1.0). (Figure 5.3.3.1).

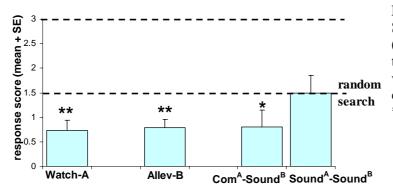


Figure 5.3.3.1. Scores of correct responses (mean + SE) in the 'B' trials in the modified versions of the social communicative condition. *: p < 0.05; **: p < 0.01

Choice behaviour in the first 'B' trials (Binomial test, test proportion: 0.5) showed a below chance performance in the 'Com^A-Sound^B' (p = 0.021) but not in the Sound^A-Sound^B (p = 0.454, ns) conditions.

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This finding provides further support for the notion that social and non-social cues are not equally effective in inducing A-not-B error in dogs. Therefore it seems that what matters is not the mere amount, but the informational selectivity of attention. That is, dogs might have extracted different kinds of information to be learnt from the communicative versus non-communicative demonstrations and this is modulated by social cognitive processes. In sum, dogs' perseverative search bias may stem from their propensity to follow human social cues rather than from inhibitory control problems or interference effects in working memory.

5.3.4. EXPERIMENT VIII/4.

A further intriguing question is whether dogs' sensitivity to human communicative signals is the evolutionary consequence of domestication. It is increasingly assumed that, during their evolution in an anthropogenic environment (and paralleled by the divergence from the wolf), dogs have become selected to display increased sociality (see above in STUDIES I & II), cooperability (STUDIES IV & V), and communicability (STUDY VI & VII). This preparedness enables the dog become sensitized to human communicative cues (Brauer et al. 2006) if the individual is properly socialized to humans (Udell et al. 2008).

This account predicts that only dogs but not human-reared wolves would respond differentially to communicative versus non-social hiding contexts in a search task. We tested this prediction in this experiment, in which we compared the performance of a different group of naïve pet dogs to that of extensively socialized, hand-reared wolves (for more details on socialization of wolves see STUDY I) in the OC and NS conditions.

METHODS

Subjects

Twelve adult pet dogs (8 males 4 females; mean age±SD: 3.9±3.5 years) of different breeds (1-1 Border collie, Labrador retriever, Hungarian vizsla, Malenois, Argentin dog and 4 mongrels) and ten hand-reared adult tame gray wolves participated (7 males, 3 females mean age±SD: 3.0±1.8 years; details about rearing conditions in STUDY I/Methods section). Three additional dogs and three wolves were excluded from the experiments because they failed to fulfil the criterion in the pre-training trials (see Procedure) or lost interest in the task by the fourth 'A' trial.

Experimental procedures

After pretraining, dogs and wolves participated in both the ostensive/communicative (OC) and non-social (NS) hiding conditions (for procedure, see above in Experiment VIII/2.). The order of the conditions was counterbalanced across subjects in both the dog and the wolf groups (within-subject design). Since wolves could not be motivated to search for toy objects, in this experiment we used a white plastic pot as target object (10 cm in diameter, 7 cm in height), baited with a piece of raw meat or cold cut for both dogs and wolves.

RESULTS & DISCUSSION

Dogs and wolves selected the baited location reliably during the 'A' trials in both conditions (mean percentage of correct choices: 95% and 88% for wolves, and 94% and 92% for dogs, in the OC and NS conditions, respectively). However, the performance during the 'B' trials differed markedly between species and contexts (Figure 5.3.4.1). A two-way ANOVA on the response scores for hiding context and species as factors revealed more correct responses in the NS than in the OC condition (F(1,20) = 15.003, p = 0.001), more correct responses by the wolves than by the dogs (F(1,20) = 4.675, p = 0.043) and a significant interaction between these factors (F(1,20) = 13.027, p = 0.002). This interaction was due to the fact that, similarly to the above results (see Experiment VIII.2), dogs selected the baited location on 'B' trials less frequently in the OC condition (t(11) = 5.043, p < 0.001), while no such effect was found in wolves (t(9) = 0.208, p = 0.840).

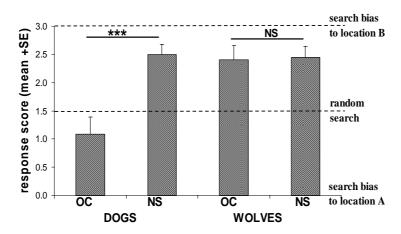


Figure 5.3.4.1. Comparison of dogs and wolves in the A-not-B task. Scores of correct responses (mean +SE) in the 'B' trials as a function of the hiding context. ***: paired t-test, p < 0.0001

The robust A-not-B error in the communicative hiding context in dogs, which was absent in extensively socialized wolves, represents a striking inter-species difference, which could be best explained by assuming that selective processes in the course of domestication of dogs led to sensitivity to human ostensive and referential signals. However, the fact that dogs, just like human infants, commit the perseverative search error when (and only when) the repeated hiding events are presented in a communicative context does not necessarily imply that this effect is mediated by the activation of the same type of interpretive bias that the ostensive cues were hypothesized to trigger in human infants (see in Experiment VIII/1.).

Evidence suggests that dogs' response to human communication is primarily driven by a motivation to satisfy ostensively cued human imperatives even when the human's action demonstration conveys inefficient or mistaken solution to goal approach (Pongrácz et al. 2004), food choice (Prato-Previde et al. 2008) or object choice (se also results in STUDY VII). These findings, along with the results presented in the current study, raise the question whether human ostensive and referential signals serve the same communicative functions in dogs as they do in human infants. If human communication is functionally interpreted as imperatives by dogs, it might be tied to the situational context, whilst infants, whose primary motivation is to learn from ostensive demonstrations, would attempt to generalize the communicative content to new situations.

5.3.5. EXPERIMENT VIII/5

As one of the crucial components of the A-not-B task is the identity of the person they interact with, in the next experiment we investigated how dogs and 10-month-old human infants react if, after the 'A' trials, the identity of the hiding person is changed and a new experimenter continues the hiding during the 'B' trials in the OC condition. If the ostensive hiding action is interpreted as an imperative order associated with a specific "instructor", we could expect the perseverative search bias to diminish during the 'B' trials, which would represent a different imperative to act on as it is given by a different person. In contrast, if the ostensive hiding action is (mis-)interpreted as conveying some generalizable information about the type of object hidden or the function of the hiding location (Csibra & Gergely 2009) that is not related to the identity of the particular demonstrator, switching the experimenter should not reduce the tendency to commit A-not-B error.

METHODS

Subjects

Twelve adult pet dogs (6 males, 6 females; mean age±SD: 2.1±1.0 years) from different breeds (2-2 Border collies, Hungarian vizslas, 1-1 Belgian tervueren, Malenois, Australian shepherd, Cavalier King Charles spaniel, Dachshund and 3 mongrels) and twelve 10-month-old human infants (5 boys, 7 girls; mean age±SD: 306.6±6.2 days) participated. Two additional dogs were excluded from the experiment because they failed to fulfil the criterion in the pre-training trials (see the procedure above in Experiment VIII/2). Four infants were also excluded from the test because they failed to pass the reaching criterion in the 'A' trial phase (see the procedure above in Experiment VIII/1).

Experimental procedures

The task included the same two phases as in Experiment VIII/2: pretraining and testing. In the pretraining trials, two women, who participated later in the test trials as experimenters, played with the subject. Therefore the two of them were equally familiar to the subject during the subsequent test phase. The experimental arrangement and the hiding procedure were similar to that of used in the OC condition of Experiment VIII/2 (for dogs) and Experiment VIII/1 (for infants). That is, during the four 'A' trials one of the experimenters performed the object manipulations using conspicuous ostensive-communicative cues. Importantly, however, after the experimenter had repeatedly hidden the toy in the 'A' trials, she left and another familiar person continued to demonstrate the hiding actions during the 'B' trials. The order of the two experimenters was counterbalanced across subjects.

Data collection and analysis

The first location that was inspected was regarded as the subject's choice and response scores were created in a similar fashion as described above (see the Data collection and analysis sections of Experiments VIII/ 1 & 2).

RESULTS & DISCUSSION

During the 'A' trials, dogs fetched the object reliably from behind screen 'A' (mean percentage of correct choices: 98%) showing a performance similar to that of found in the OC condition of Experiment VIII/2 (94%). Infants also searched for the toy correctly in the majority of 'A' trials (82%) replicating the success rate (88%) reported in Experiment VIII/1 in the same ostensive-communicative hiding context. However, infants and dogs responded to the new experimenter in the 'B' trials differentially (Figure 5.3.5.1).

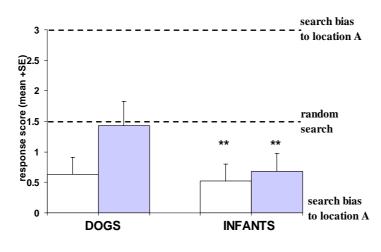


Figure 5.3.5.1.

Dogs and 10-month-old infants respond differentially to the switch of the experimenter in the ostensive communicative hiding context. Left (white) columns indicate correct responses (mean +SE) with the same experimenter (data from Experiment VIII/2 (dogs) and from Experiment VIII/1 (infants). Right (shaded) columns indicate the performance during the

'B' trials in the Experimenter-switch condition (Experiment VIII/5). **: one sample t-test, p < 0.02 in comparison to the success rate expected by random search (0.5 x 3 'B' trials).

Infants displayed a perseverative search bias to reach to location A, and their success rate was significantly below chance level (t(11) = 2.932, p = 0.014). In contrast, dogs did not show a significant search bias towards the empty 'A' location (t(11) = 0.103 p = 0.920), suggesting that they did not generalize to the new situation in the 'B' trials what they had learnt during the 'A' trials.

These results show differential influence of changing a basic stimulus parameter (the identity of experimenter) on dogs' and human infants' tendency to commit the perseverative search error. The finding that, compared to the OC condition in Experiment VIII/2 dogs did not perseverate after switching the experimenter is consistent with the hypothesis that dogs anchor communication to the specific situation, and especially to the specific communicator who is ostensively addressing it to them. At the same time, and unlike in the NS condition of Experiment VIII/2, dogs were not always successful in finding the object hidden by the new experimenter. Their random search pattern indicates that the unchanged aspects of the situation (same object, same room, same screen, etc.) carried sufficient cues of the previous context to confuse them, and suggests that it is the overall similarity of the test situation to the training situation that determines whether dogs extend the scope of the learned imperative to the new context. Crucially, the human who ostensively communicates towards the dog forms an indispensable element of the context. For infants, however, it does not seem to matter who performs the ostensive hiding demonstration, and they readily generalize their erroneously learnt object-finding action to the new person context.

5.3.6. STUDY VIII. GENERAL DISCUSSION

Results of the infant study (Exp. VIII/1) are not compatible with the currently widely accepted explanations for the A-not-B perseverative response bias that attribute this robust developmental phenomenon to the dominance (and lack of inhibition) of the prepotent motor search response. These results also challenge recent proposals that the motor priming of the prepotent response can be induced by simply observing the manual hiding actions directed at location 'A', mediated by the mirror neuron system (Longo & Berthental 2006), because the NC context provided the same amount of visual (as well as motor) experience of the repeated manual hiding actions directed at container 'A' as did the OC context.

Human infants are highly social creatures (Hermann et al. 2007) who cannot help but interpret the ostensive communicative signals directed to them. Although such a disposition prepares them to efficiently learn from adults, in certain situations, like the A-not-B task, it can also misguide their performance. Our demonstration of the social communicative determinants of infants' early tendency for perseveration in motor search tasks provides independent support for the natural pedagogy hypothesis (Csibra & Gergely 2009) suggesting that sensitivity to ostensive-referential communication is a basic evolutionary adaptation that is fundamental to the emergence of human social cognition.

Results of the second experiment show an apparent behavioural analogy between human infants and dogs. In both species, one of the most important causal factors leading to perseverative search errors is the communicative ostensive-referential context. The seemingly mistaken response, called A-not-B error, is not (or at least not only) due to insufficient attentional and motor functioning, but paradoxically, may be indicative of sophisticated social competence in both dogs and human children.

We have already provided evidence (see STUDY VII) that domestic dogs readily adopt inefficient responses in object choice tasks as a result of repeated observations of human action demonstrations, and their sensitivity to human social cues may lead to apparently faulty behaviours (see also Kaminski 2009). Such a disposition, which may result from the domestication of dogs and/or from their extensive experience with humans, is likely to prepare dogs to efficiently learn from humans in a wide range of situations. These claims are further confirmed by Exp. VIII/3 showing that dogs' erroneous responses in the A-not-B task do not arise from inhibitory control problems or interference effects in working memory but can be altered by changing the location of ostensive cueing.

The lack of a similar sensitivity to human ostensive-communicative signals in extensively socialized wolves (Exp. VIII/4) supports the view that this is an evolutionary novel skill in the Canis genus providing a typical case for convergent social evolution (as the consequence of domestication) between man and dog. However, it seems that the precise function of the cognitive-interpretive mechanisms elicited by communication differs between dogs and humans. For infants, ostensive and referential communicative signals serve a primarily epistemic function by indicating an opportunity to acquire culturally shared knowledge about referent kinds (Csibra & Gergely 2009). Dogs' sensitivity to these signals is parasitic on human communication by exploiting them for a different function: to give orders to perform some specific action at a referentially indicated particular location in the presence of (and "for") a specific person presenting the imperative.

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In summary, dogs' behaviour in the A-not-B error task probably driven by a combination of factors, including sensitivity toward human ostensive signals and our findings raise the possibility that dogs' response to human communication is primarily driven by a motivation to satisfy ostensively cued human imperatives even when it leads to an inefficient or mistaken solution (see also STUDY VII above).

5.4. STUDY IX. CONSTRUCTION SKILLS - KNOWLEDGE ATTRIBUTION AND MINDREADING*

Abstract

The main goal of this study was to investigate if dogs are able to discriminate between request tasks in which the human Helper has different knowledge states concerning the whereabouts of the reward and/or the tool, relying upon the Helper's engagement/disengagement in the hiding processes of the two objects.

In the first experiment the behaviour of adult pet dogs was compared to that of 2.5-year-old children tested in the same nonverbal "mental attribution" task in which a human Helper's knowledge state regarding the whereabouts of a hidden toy and a stick (a tool necessary for getting the out-of-reach toy) was systematically manipulated. In the four experimental conditions the Helper either participated or was absent during hiding of the 'Target Object' (toy) and the 'Tool' (stick) and therefore she knew the place(s) of (1) both the Target Object and the Tool, (2) only the Target Object, (3) only the Tool or (4) neither of them. The subjects observed the hiding processes, but they could not reach the objects, so they had to involve the Helper to retrieve the Target Object. Both dogs and children signalled the place of the toy more frequently if the Helper had been absent during toy-hiding compared to those conditions when she had participated in the hiding. However, unlike children, dogs indicated the location of the stick only sporadically. In those conditions in which the Helper was ignorant of the whereabouts of only one of the objects the children indicated the place of this object more often than that of the known one.

Although both dogs' and children's behaviours appear to correspond (at least partially) with the Helper's knowledge state; even the subtle distinction made by the children can be interpreted without a casual understanding of knowledge-formation in others.

In the framework of a longitudinal case study on a specially trained service dog, Philip, the second experiment was aimed to get a more sophisticated insight into the cognitive functioning of the dog's mind. We used the same 'Ignorant Helper' paradigm as in the first experiment, in this case, however, the procedure was identical to that used in an ape-study (Dona, the orang-utan: see - Gomez & Teixidor 1992) and therefore provides the possibility for direct dog-ape comparison regarding their performance. Results show that similarly to the case with this "enculturated" orang-utan, after few trials Philip was able to adjust his communicative behaviour to the state of knowledge of his human partner and cooperated successfully in the problem solving task. Although the exact mechanism underlying this communicative behaviour is still not clear, this approach gives a new possibility to conduct comparative studies aimed to understand the evolution of social cognition.

*Based on:

Virányi, Zs., Topál, J., Miklósi, Á., Csányi V. (2006). A nonverbal test of knowledge attribution: a comparative study on dogs and human infants. Animal Cognition 9(1): 13-26.

Topál, J., Erdőhegyi, Á., Mányik, R., Miklósi Á. (2006). Mindreading in a dog: an adaptation of a primate 'mental attribution' study. International Journal of Psychology and Psychological Therapy 6: 365-379.

INTRODUCTION

The recognition of another individual's mental state is a sophisticated form of social competence as being manifestation of "distributed cognition" (Johnson 2001). Since Premack and Woodruff's seminal study (1978) the question of mental state attribution in nonhuman species has been in the focus of heated debates (see e.g., Povinelli & Vonk 2003; Tomasello et al. 2003a, b). Studies investigating what chimpanzees know about seeing (see Call 2001b for review) have provided the strongest body of results supporting the hypothesis that chimpanzees understand "at least some psychological states of others" (Tomasello et al. 2003a).

Recently, the dog has been proposed to be a promising species for studying the evolutionary emergence of social cognition (see Part I for review) and several lines of research suggest that dogs may have evolved some special social skills for understanding cues of human communication (see e.g., the findings by Studies I-VIII above). Accordingly, the question arises if dogs' social cognitive skills go beyond relying on humans' behavioural cues and reach to some deeper understanding.

To study mental state attribution in nonhuman animals three basically different non-verbal methods have been developed: "Guesser-Knower" (e.g. Call et al. 2000), "Competitive Conspecific" (e.g. Hare et al. 2001) and "Ignorant Helper" (Gomez 1998, Whiten 2000) paradigms. These studies were designed to assess if subjects (mainly primate species) understand the casual connection between past perception and present knowledge and/or whether subjects are able to take their partners' previous experience or perceptual access into account.

The 'Ignorant Helper' design (Gomez & Teixidor 1992; Whiten 2000) tests the subjects' sensitivity to others' past visual access in an object-specific way. Both studies involved human-raised apes (one orang-utan and three chimpanzees respectively) with human contributors in a cooperative situation in which the ape could get some out-of-reach food by indicating it to a human partner. The essence of this design is that two relevant objects—a piece of food and a tool necessary for getting the food—are involved in the procedure. To make it obvious, the subjects receive several warm-up trials, in which the cooperative human partner (the Helper) uses the tool to get the food that was hidden by another human (the Hider) and provides the food to the subject if it indicated the correct location of food (simple request task). Following the warm-up sessions, probe trials are introduced in which the Helper's knowledge about the locations of the food and the tool is systematically manipulated. That is, the Helper may be ignorant of either the location of both the food and the tool, or the food only, or the tool only, or none of them. Importantly, however, neither of these studies involved all of the four possible combinations of the Helper's knowledge regarding the food and the tool (i.e. food only, tool only, both food and tool, neither of them).

In the first experiment we used a modified version of Whiten's (2000) study to measure dogs' and children's behaviour in conditions representing all possible combinations of settings. In the second experiment we replicated the Gomez & Teixidor (1992) study on Dona, the orang-utan with a specially trained service dog that had been trained to assist his disabled owner.

5.4.1. EXPERIMENT IX/1

The main goal of the first experiment was to investigate if dogs are able to discriminate between request tasks in which the human Helper has different knowledge states concerning the whereabouts of the reward and/or the tool, relying upon the Helper's engagement/disengagement in the hiding processes of the two objects and to compare their behaviour to that of 2.5-year-old children tested in the same conditions. Children of this age were selected to make comparisons with dogs in this situation because evidence for mental understanding of causal intentions starts to accelerate around the end of the second year, with the comprehending pretence in others, a systematic understanding that visual attention causes knowledge, and the routine use of protodeclarative gestures to induce or modify intentional states in others appear (Wellman & Phillips 2001). A mature understanding of mental agency (i.e., naive theory of mind) however, is still not present at this age because a number of studies report that this ability arises around 4 years of age (see Perner 2000 for review).

METHODS

Subjects

Eleven adult pet dogs (5 females, 6 males; mean age: 4.9 years, range: 1–10 years) and 11 children (5 girls, 6 boys; mean age: 29.4 months, range: 26–35 months) participated in the experiment. The dogs were from five different breeds (3 Belgian tervuerens, 2 German vizslas, 1-1 Boxer, Sharpei, Malinois) and three mongrels. Only dogs living in the flat together with their owners and keen on retrieving objects and playing with toy were selected. All the owners were women, their age ranged between 20 and 35 years. All children were from Hungarian middle-class families. Five additional children were excluded from the study because of motivational problems and/or because their mothers neglected the instructions in course of the experimental trials.

Experimental procedures

Testing was done in a familiar room (minimal size: 3×5m) of the subjects' home (Figure 5.4.1.1). A stick (1 m long) was placed out of reach of the dog/child in a position (standard place) where it could not be seen by the Helper from her predetermined position, which was indicated by a chair. The experimenter also determined four additional hiding places for the stick and three hiding places for the toy where the hidden objects were out of reach of the dog/child. The hiding places were located under (or on top of) heavy pieces of furniture (e.g. bed, cupboard, book case) from where the dog/child could not get the toy/stick out. The distance between any two possible hiding places was at least 1.5 m. The Helper's chair was positioned in a way that she could see the entire room (all hiding places) from there.

For the dogs, the hidden object was a favourite toy (e.g. tennis ball) whilst the toy was chosen by the children from a set of rollable toys (mainly small cars and balls), which were offered by the experimenter prior to the experiment. The owners/mothers did not know the scientific goal and the hypothesis of the study in advance; they were informed that its purpose was investigating the manners of the dog/child-human communication in nonverbal situations. Before the experiment the

experimenter thoroughly instructed the owner/mother about the experimental trials, the owner/mothers received written instructions as well. The children were told only that the experimenter came to play a rolling game with them and their mothers.

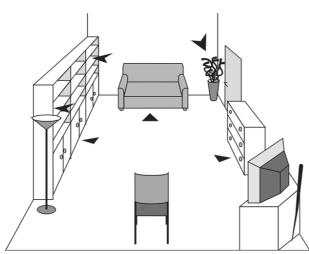


Figure 5.4.1.1.

The experiment took place in a room of the subject's home. The picture example. In shows one foreground a chair is positioned for the Helper and the stick is in its usual place (behind the TV). In the background, on the right side the door can be seen where participants can enter and leave the room. The triangles sign the hiding places for the toy and for the stick (>): three-three out-of-reach hiding places for both of the objects.

Warm up play session (retrieval tasks and toy hiding trials)

In order to make the dogs and children familiar with the experimental situation and to make them familiar with the use of stick and the toy, 'Warm up play sessions' were introduced. Because we assumed that dogs had less experience with sticks and their use, 7 consecutive daily sessions with 3 trials in each were run in the case of the dogs and only a single 3-trial session was provided for the children. The procedure of the warm up trials was also different to some extent for the dogs and the children.

1st step: The owner/mother initialized playing with the dog/child

In case of the dogs, the owner first put the toy into one of the three predetermined hiding places and then called the dog by its name. When the dog responded, the owner tried to reach the toy with her hand 3-4 times unsuccessfully. Then she went to the stick, took it from its standard place and got the ball with it. Finally, she replaced the stick, called the dog and initiated a retrieval game. In case of the children, the mother took the toy that the child had just chosen, sat down on the floor, called her child and initiated playing with the toy (she said: "I roll it, you have to catch it!").

2nd step: Three consecutive warm up trials

The owner stood and threw the ball at a distance of 2–3 m and encouraged the dog to retrieve it (the mother and the child bowled the toy to each other while sitting on the floor facing each other). After the dog retrieved the toy at least three times (after bowling the toy to each other at least three times) the owner (mother) threw/rolled the toy into one of the three predetermined hiding places apparently by accident. From here the dog (child) could not retrieve the toy, so the owner (mother) went there and tried to reach the toy with her hands but did not succeed. Then she went to the standard place of the stick, removed it from its place and got the toy with it. She called the dog (child) if she/he/it was not attending to her actions. After

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replacing the stick the owner (mother) resumed playing with the subject and the next warm up trial started with the same procedure, except that the toy was thrown/rolled into another hiding place. In the three warm up trials the toy was rolled "accidentally" into each of the three hiding places.

The first warm up session was made in the presence of the experimenter who corrected the owner's (mother's) behaviour if it was necessary. The next six sessions were completed by the owner, and on the eighth day the experimental trials followed. The children received only one warm up session, and the experimental trials were executed on the same day.

Experimental trials

Following the warm up sessions four experimental conditions were introduced in which both the owner/mother (who played the role of the Helper) and the experimenter (playing the role of the Hider) participated. Importantly, experimental situations were designed so that the Helper's knowledge concerning the whereabouts of the Tool (stick) and the Target object (toy) were systematically manipulated and all trials consisted of 6 different phases (see Figure 5.4.1.2).

(1) Entering phase: All experimental trials began in the same way: the Helper (owner/mother), the Hider (experimenter) and the subject (dog/child) entered the room. The next two phases, however, were different in the different conditions based on the timing of the Helper's leaving and re-entering the room:

'Introductory Stick & Toy' condition (The Helper participated in hiding of both the stick and the toy.)

- (2) Stick-hiding phase: The Hider called to the subject to gain his attention ("Name + Look here!" was said to the dogs and "I will play with you, but before, please, look what we are doing!" was told to the children). Then the Hider and the Helper went to the place of the stick, removed the stick into one of the four predetermined hiding places. The Hider called the subject if he was not attending to the actions.
- (3) Playing and toy-hiding phase: Following this, the Helper sat down (the owners sat on their chair, the mothers sat on the floor in front of their chair), and the Hider took the toy out from her pocket and staying standing and throwing the toy to the dog or sitting down on the floor forming a triangle with the child and the Helper and rolling the toy to the child initiated retrieval/rolling game with the subject in a way which was similar to that was played in warm up trials. In this case, however, the Hider was also involved to the game: The Hider threw/rolled the toy alternately to the subject and the Helper. (The dogs fetched the toy while the children and the Helper threw/rolled it back to the Hider.) When the Hider got the toy back for the third time, she threw/rolled it into one of the three predetermined hiding places apparently by accident. She looked at the subject, shrugged her shoulders ("Oh sorry!" she said) and finally left. The Helper stayed in the room.

'Toy only' condition (The Helper participated only in the hiding of the toy.)

(2) Stick-hiding phase: After spending a few seconds together in the room the Helper left saying to the subject: "I will come back soon, stay here!". Then the Hider called the subject ("Name + Look what I am doing!") and went to the place of the stick, removed it and put it into one of the four predetermined hiding places. Care

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was taken that the subject was clearly attending and following each step of manipulation.

(3) Playing and toy-hiding phase: After hiding the stick the Hider went to the door, opened it and invited the Helper into the room. After the Helper sat down the Hider played with the subject and the Helper, and hid the toy in the same way as described in the 'Stick and Toy' trial.

'Stick only' condition (The Helper participated only in the hiding of the stick.)

- (2) Stick-hiding phase: After entering the Helper stayed in the room and participated in hiding the stick in the same way as described in the 'Stick and Toy' trial
- (3) Playing and toy-hiding phase: After hiding the stick, however, the Helper left the room saying: "I will come back soon, stay here!". After the Helper closed the door the Hider took the toy out from her pocket and initialized a fetching/rolling game with the dog/child which was similar to that played in warm up sessions. After throwing/rolling the toy to the subject three times, the Hider threw the toy into one of the three predetermined hiding places apparently by accident. She looked at the subject, shrugged her shoulders ("Oh sorry!" she said) and left. At the same time the Helper entered.

'Neither' condition (The Helper did not participate in the hidings of either of the stick and the toy.)

- (2) Stick-hiding phase: After spending a few seconds together in the room the Helper left in the same way as in the 'Toy only' condition, so the Hider hid the stick on her own while calling the subject's attention to these actions (see 'Toy only' condition).
- (3) Playing and toy-hiding phase: After hiding the stick (without inviting the Helper into the room) she took the toy out from her pocket and played with the subject and hid the toy in the same way as in the 'Stick only' condition. Then she left the room but in the same time the Helper entered. From this point on all experimental trials continued in the same way.
- (4) Waiting phase: After the Hider's disappearance, the Helper sat on the chair at her predetermined place for 30 s without saying anything and followed the subject with her attention by turning only her head. Looking in other directions than the subject was not allowed; she had to focus her attention on the subject only.
- (5) Object retrieval phase: After 30 s had passed, the experimenter knocked at the door, and the Helper retrieved the stick and the toy as soon as possible. To achieve this she could rely on her knowledge if she had participated in hiding any objects and/or on the subject's behaviour during the waiting phase (behaviours indicating the place of the objects) and/or she could visit systematically the possible pre-determined hiding places (known-well by the Helper). Importantly, when searching for the objects, the Helper had been asked to ignore the subject, and verbal communication was not allowed to prevent the subject from receiving feed back with regard to his/her behaviour. When the Helper got the stick she had to work the toy off by the help of the stick and then to replace the stick to its original, standard place as soon as possible.

(6) Playing phase: After the Helper got the toy and replaced the stick she initiated a short fetching/rolling game with the subject.

	1, STICK & TOY condition	2, TOY ONLY condition	3, STICK ONLY condition	4, NEITHER condition	
Phase 1: Entering	Hel	per, Hider and Su	bject enter the roo	om	
	Helper, Hider	Helper leaves		Helper leaves	
Phase 2: Stick-hiding	& Subject	Hider &	Helper, Hider	Hider &	
r hase 2. Suck-munig	& Subject	Subject	& Subject	Subject	
		Helper enters	Helper leaves		
	Helper, Hider	Helper, Hider	Hider &	Hider &	
Phase 3: Toy-hiding	& Subject	& Subject	Subject	Subject	
Filase 5. Toy-maing	Hider leaves				
			Helper enters	Helper enters	
Phase 4: Waiting	Helper & Subject				
Phase 5: Retrieving	Halman & Cubicat				
the stick and the toy	Helper & Subject				
Phase 6: Playing	Helper & Subject				

Table 5.4.1.1. Experimental schedule for the four experimental conditions based on the presence of the three participants. All trials began and terminated in the same way, the Helper, however, left and re-entered the room in different phases of the different conditions and accordingly she participated in hiding 1) both the stick and the toy, 2) only the toy, 3) only the stick or 4) none of them.

All dogs and children were observed in all four types of conditions in a session with 3–5 min breaks between the trials. The first experimental trial was the 'Introductory Stick and Toy' condition for all subjects since this condition — having the owner/mother continuously present — was the most appropriate to introduce the novel elements of the experimental situation (playing with the Hider, etc.). The order of the other three conditions and also the hiding places of the stick and toy in all four trials were randomised and predetermined. The children received only one session, however the dogs were re-tested on the subsequent day in similar way except that the order of all four trials were randomised. In this way the children participated in one trial of each condition whereas the dogs received two trials of each condition on two consecutive days. Experimental trials were recorded by two video cameras in fixed positions and the behaviour of the subjects was analysed later.

Data collection and analysis

The behaviour of the dogs and the children was observed during the waiting phases of the experimental conditions (i.e. in the half a minute when the Helper was passive and looked at the subject attentively) and the analysis was focused on the "indicative behaviours" of the subjects. In line with earlier studies (Hare et al. 1998; Miklósi et al. 2000; O'Neill 1996) gaze-alternations between the toy/stick and the Helper and gazing at the toy/stick accompanied by vocalization (barking, whining) in dogs and verbal communication in children were defined as indicative behaviours. In the case of human infants, pointing (with extended arm) at the place of the toy/stick (while the child was either looking at the place of the object or at the mother) was also regarded as signalling behaviour. Gaze-alternation was defined as behaviours

when gazing at the Helper (owner/mother) was followed directly by a gaze at the place of the toy/stick or vice versa. We should note that children (and dogs) often combined different types of signalling behaviours and gaze alternations. For example children often alternated their gaze from their mother to the place of the toy, pointed to it and said "Give it to me!" at the same time. In these cases the different types of signalling overlapping in time were counted as one single indication. The direction of gazing was recorded on the basis of head/face orientation of the dogs/children. In accordance with these definitions the number of indicating behaviours (behaviours referring to the goal objects) was measured later from the videotapes separately toward the toy and the stick. Reliability of measuring the direction of gazing and the direction of pointing was assessed by means of parallel coding of the 25% of the total sample by two observers, one of whom was blind to the experimental condition. Their inter-observer agreement yield the Cohen kappas of 0.90 for the dogs' orientation, 0.90 for the children's gazing direction and 0.99 for the children's pointing direction.

In order to analyse whether the presence or absence of the Helper during changes of the location of the toy/stick had a functionally relevant effect on subject's behaviour, we recorded both the focus and the sequence of indicative behaviours (i.e. what is indicated and what the sequence of indication is if more than one location is indicated). In line with this approach (e.g. Gomez 1998), the 'Scores for situation-relevant signalling' were established for the different experimental conditions as shown in Table 5.4.1.2.

CONDITION	SCORES FOR RELEVANT SIGNALLING BEHAVIOUR				
	1	0	-1		
Stick & Toy	No signalling behaviour	Indicating either the	Indicating both the		
		place of the toy or the	place of the toy		
		stick	and the stick		
Toy only	Indicating only the place	No signalling behaviour,	Indicating only the		
	of the stick,	or indicating first the	place of the toy		
	or first the place of the	place of the toy and then			
	stick and then the toy	the stick			
Stick only	Indicating only the place	No signalling behaviour,	Indicating only the		
	of the toy,	or indicating first the	place of the stick		
	or first the place of the	place of the stick and			
	toy and then the stick	then the toy			
Neither	Indicating both the place	Indicating either the	No signalling		
	of the toy and the stick	place of the toy or the	behaviour		
		stick			

Table 5.4.1.2. Establishing the 'Scores for situation-relevant signalling' in the four experimental conditions based on which object(s) the dog/child indicated in which order.

Score 1 was given if the subject's signalling behaviour was properly adjusted to the knowledge state of the Helper.

Score 0 was given if the subject's signalling behaviour gave only partial information needed by the Helper (i.e. signalled only one of the unknown hiding places) or provided the necessary information only after giving unneeded information.

Negative score (-1) was given when the subject signalled only the location of the object(s) known by the Helper.

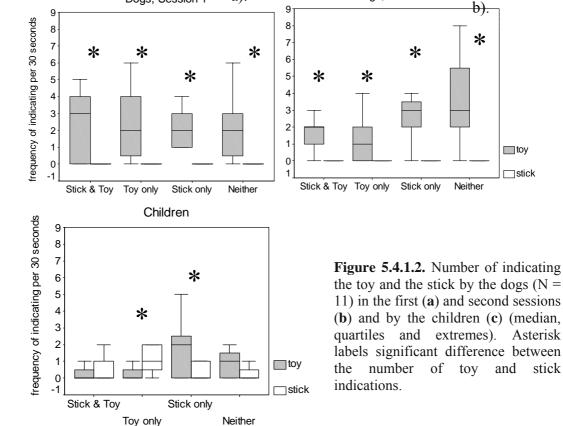
Because variables were not distributed normally, nonparametric statistical methods (Friedman ANOVA, Mann-Whitney U test, Wilcoxon matched pairs signed rank test) were used for the data analyses.

RESULTS

Frequency of indicating behaviours towards the goal objects (toy and stick)

To determine if the subjects indicated the location of the specific object(s) of which the Helper was ignorant more intensively than the location of the object(s) of which she was knowledgeable, frequency of the toy-indicating and frequency of stick-indicating behaviours in the same condition were compared. The dogs were found to signal the place of the toy significantly more often than the place of the stick in all conditions (Wilcoxon matched pairs signed rank tests, p < 0.02 in each condition for both sessions; Figure 5.4.1.2a, b). In contrast, the children tended to show toy- and stick indicating with similar intensity in those trials in which the Helper knew the places of both objects or neither of them (Z(11) = 0.0; p = 1.00) for 'Stick & Toy' and Z(11) = -1.20; p = 0.23 for 'Neither' condition). In trials however, in which the Helper knew either the whereabouts of the stick or the toy, the children tended to show more indicating behaviours toward the place of the object which was unknown to the Helper (indicating the toy more frequently than the stick in 'Stick Only' condition: Z(11) = -2.2; p = 0.028; and indicating the stick more frequently than the toy in 'Toy Only' condition: Z(11) = -1.99; p = 0.046; Figure 5.4.1.2c, see also Table 5.4.1.3).

Dogs, Session 2



a).

Dogs, Session 1

□ toy

□ stick

	_	Experimental condition			
	Indicating	STICK &	TOY	STICK	NEITHER
	the	TOY	ONLY	ONLY	
DOGS	Toy	7 (64%)	8 (73%)	11 (100%)	8 (73%)
1 st session	Stick	1 (9%)	1 (9%)	2 (18%)	0 (0%)
DOGS	Toy	9 (82%)	7 (64%)	10 (91%)	10 (91%)
2 nd session	Stick	2 (18%)	1 (9%)	1 (9%)	1 (9%)
	Toy	3 (27%)	3 (27%)	7 (64%)	7 (64%)
CHILDREN	Stick	3 (27%)	8 (73%)	4 (36%)	3 (27%)

Table 5.4.1.3. Number (and percentage) of the dogs (N = 11) and children (N = 11) who indicated the toy or the stick in the different experimental conditions

To analyse separately if subjects tailored their toy indicating behaviour to the Helper's knowledge state of the location of the toy and their stick-signalling behaviour to the Helper's knowledge state of the place of the stick the intensity of signalling an object was compared in the different conditions. Comparisons of the frequencies of indicating the toy across the four experimental conditions did not show significant differences in the first session for the dogs (Friedman ANOVA: $chi^2(3) = 1.500$; p = 0.682), but the dogs in the second session and the children performed significantly different frequency of toy-indicating as a function of experimental condition ($chi^2(3) = 10.402$; p = 0.015 for the dogs and $chi^2(3) = 9.592$; p = 0.022 for the children). Considering the number of stick-indicating behaviours there were no significant differences among the four different conditions (dogs, first session: $chi^2(3) = 2.00$; children: $chi^2(3) = 5.535$; p=0.137).

Similar results were found when the number of toy indicative actions were summed for conditions in which the Helper was knowledgeable regarding the location of the toy ('Toy-Knowledgeable' trials = 'Stick & Toy' + 'Toy Only') and in conditions in which she was ignorant ('Toy-Ignorant' trials = 'Stick only' + 'Neither') and were compared to each other. 'Toy-Knowledgeable' and 'Toy-Ignorant' conditions did not show significant difference for the dogs in the first session (Z(11) = -0.62; p = 0.535) but both dogs in the second session (Z(11) = -2.81; p = 0.005) and children (Z(11) = -2.719; p = 0.007) were found to signal the toy more frequently if the Helper was ignorant of its location (Figure 5.4.1.3a). A similar analysis based on the Helper's knowledge about the place of the stick ('Stick-Knowledgeable' trials = 'Stick & Toy' + 'Stick Only' versus 'Stick-Ignorant' trials = 'Toy only' + 'Neither') showed no significant differences in either the dogs (Z(11) = -1.0; p = 0.317 and Z(11) = -0.38; p = 0.705 in the first and second session) or the children (Z(11) = -1.41; p = 0.158) (Figure 5.4.1.3b).

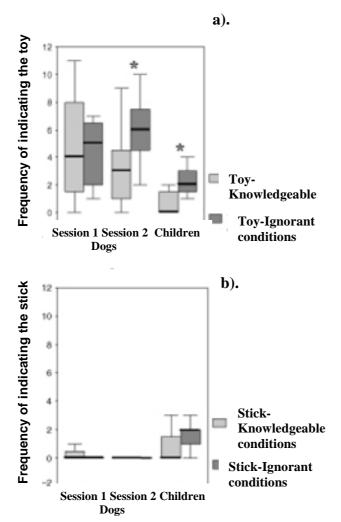


Figure 5.4.1.3. (a) Sum numbers of indicating the toy in the two Toy-Knowledgeable ('Stick & Toy' + 'Toy only') and the two Toy-Ignorant ('Stick only' + 'Neither') conditions (median, quartiles and extremes). (b) Sum of numbers of indicating the stick in the two Stick-Knowledgeable ('Stick & Toy' + 'Stick only') and Stick-Ignorant ('Toy the two only'+'Neither') conditions (median, quartiles and extremes). Asterisk labels significant difference between the Knowledgeable and the Ignorant conditions (Wilcoxon matched pairs test

Scores for situation-relevant signalling

In principle, the question of whether or not the subjects' indicating behaviour shows some understanding of the connection between the presence/absence of the Helper (when stick/toy was hidden) and her knowledge/ignorance can be answered by the analysis of individuals' mean scores gained in the four conditions. Interestingly, a comparison based on this consideration did not show significant differences between the dogs' and the children's overall performance (Mann Whitney U test, $N_1=N_2=11$, U = 39.0; p = 0.171 for the comparison between children and dogs in the first session, and U = 36; p = 0.116 for the comparison between children and dogs in the second session). However, if the children's and the dogs' performance was compared in all four conditions separately (Figure 5.4.1.4) this similarity appeared only in the 'Stick & Toy' (U = 46.5; p = 0.365 and U = 38.0; p =0.151 for the first and second session respectively) and 'Neither' trials (U = 52.5; p =0.606 and U = 55.5; p = 0.748 for the first and second session respectively). Importantly, however, the children showed significantly more relevant indicating behaviour in the 'Toy only' condition (U = 15.5; p = 0.002 and U = 18.0; p = 0.004 for the first and second session respectively), in which the 'situation-relevant' behaviour was indicating the stick, or first the stick and then the toy. In contrast, in the 'Stick only' condition, the dogs out-performed the children in the first session (U

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= 27.5; p = 0.028) although in the second session their scores were not significantly higher than those of the children (U = 40.5; p = 0.193) (Table 5.4.1.4).

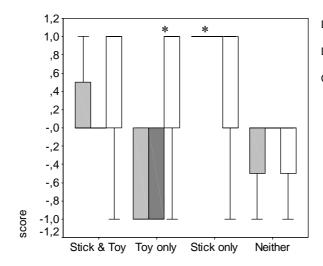




Figure 5.4.1.4 Scores for situation-relevant signalling. Mean scores of dogs (in session 1 and 2) and children gained in the four experimental conditions (median, quartiles and extremes).

	Experimental condition			
	STICK & TOY	TOY ONLY	STICK ONLY	NEITHER
CHILDREN	7 (64%)	6 (55%)	5 (46%)	2 (18%)
DOGS	3 (27%)	0 (0%)	11 (100%)	0 (0%)
1 st session				
DOGS	2 (18%)	0 (0%)	9 (82%)	1 (9%)
2 nd session				

Table 5.4.1.4. Number (and percentage) of dogs and children who performed 'situation-relevant signalling' behaviour (received score 1) in the different experimental conditions.

There was another difference between the performance of dogs and children shown in scores for situation-relevant signalling. The children did not show differences in their scores as a function of experimental conditions (Friedman ANOVA, $chi^2(3) = 6.0$; p = 0.112). The dogs, however showed striking differences in both sessions (first session: $chi^2(3) = 21.35$; p < 0.0001; second session: $chi^2(3) = 19.35$; p = 0.0002). That is, the dogs performed more relevant behaviour in 'Stick only' trial compared to 'Toy only' condition (Dunn's post hoc test, p < 0.01).

DISCUSSION

Although significant differences were not found in the overall performance of the two experimental groups, only the dogs' performance varied extremely as a function of experimental condition. Whilst the dogs' behaviour appeared to be highly relevant in the condition in which the Helper was ignorant regarding the whereabouts of the toy ('Stick only' condition), they show less relevant signalling in the other conditions (predominantly indicated the place of the toy). This is so because they indicated more often the place of the toy compared to the place of the stick in all experimental conditions.

Children, however, showed object-specific changes in their signalling behaviour. They showed similar frequency of indicating the toy and the stick in trials in which the Helper had the same information regarding the whereabouts of the toy and the stick (i.e. either participated or not in the hiding of both objects — 'Stick & Toy' and 'Neither' conditions). In trials however, in which the Helper had information only about one of the objects ('Toy only' and 'Stick only' conditions), the children specifically signalled the object more often the location of which was ignored by the Helper (more stick-indicating than toy-indicating in 'Toy only' condition and more toy-indicating than stick-indicating in 'Stick only' condition). These findings are consistent with other studies (O'Neill 1996; Dunham et al. 2000) showing that children as young as age 2.5 may be able to take into account which events their partner has witnessed and to tailor their communication accordingly.

Comparing the dogs' performance to that of the children, one of the most striking differences is the infrequency of stick-indicating behaviours in dogs. One could assume that this relates to the species-specific differences in their object-manipulation abilities. Namely, 2.5-year-old children are predisposed to be more skilful in problem situations involving tool-use. Children, undoubtedly, have a lot of individual experience in using and manipulating objects as tools. All of the human participants have already practiced using different stick-like objects to retrieve other objects from out-of-reach places before the experiment whereas dogs had only indirect experiences of these actions via observing humans. Accordingly, dogs had difficulties in recognizing the role of the stick in getting the toy, and the warm-up trials were insufficient to establish this relationship between the stick and the toy.

Moreover, the lack of interest in the stick in dogs may be the result of the different "motivational value" of the two goal objects (stick and toy). Dogs (unlike children) were probably over-motivated in order to get the toy, and therefore they were less attentive when the stick was manipulated and hidden. As a consequence, they were less motivated to show behaviours referring to the place of the stick. It should be noted that any of the combination of the aforementioned possibilities could be responsible for why the dogs indicated predominantly the place of the toy but not the stick in all conditions.

Going beyond the question of which object the subjects chose to signal more intensively, the frequencies of indicating a special object were compared in the pair of trials when the Helper was knowledgeable of the place of this certain object to the other, ignorant pair of trials in order to test if the subjects communicated about a certain object more intensively when the Helper was ignorant of the place of this object.

This analysis showed that the children adjusted the frequency of their toy-indicative behaviour to the Helper's previous participation/absence in hiding the toy but the Helper's knowledge regarding the whereabouts of the stick did not influence the frequency of the stick-indicating behaviours. However, given that children younger than three year old show only limited ability of mental state attribution (e.g. Wimmer et al. 1988; O'Neill et al. 1992), the 2.5-year-olds' performance in this study still seems to be beyond expectation. In fact, the ability to solve conceptual perspective taking or theory of mind problems is believed to show a significant developmental improvement in human infants between 3 and 4 years of age (e.g. Chandler et al. 1989). Some suggest however, that the traditional theory of mind tasks relying on verbal skills underestimate younger children's abilities (see O'Neill 1996, for review) because mind-reading skills manifest in nonverbal behaviour (e.g. gazing, pointing) earlier than children become able to perform it explicitly in their

verbal responses (e.g., Garnham & Ruffman 2001; Carpenter et al. 2002b; Kovács et al. 2010).

Although the dogs hardly showed any stick related behaviours and even their toy-indications were not influenced by the experimental conditions in the first session, in the second session they proved to be sensitive to the fact that the Helper had or had not participated in the hiding of the toy (less signalling when the Helper participated in the hiding of the toy). It is quite unlikely that this change in the dogs' behaviour from the first session to the second one was the result of quick trial-anderror learning because the dogs did not receive any feedback from the Helper in the course of the trials (i.e. any reinforcement about the appropriate action). Apart from trial-and-error learning, subjects might have learnt about the general meanings of the experimental situation. For example they may have learnt that the Helper is ready to get the toy and to play with them even in those conditions when she had not participated in the retrieval game and in hiding of the toy ('Stick & Toy' and 'Toy only' conditions). Therefore, facing an already familiar situation, the dogs in the second session behaved in a more active, initiating way, which resulted in indicating the place of the toy more intensively if the Helper had not participated in hiding the object.

In summary, like children, dogs (at least to a certain extent) may be able to tailor their communicative behaviour to their partner's previous participation/disengagement in conspicuous events. The adequate changes in the frequency of indication of the toy in dogs may mirror a fast "insightful process" learning (Gomez 1998) rather than trial-and-error mechanism.

5.4.2. EXPERIMENT IX/2

In the framework of a longitudinal case study on a specially trained service dog, Philip, the second experiment is aimed to get a more sophisticated insight into the cognitive functioning of the dog's mind. We use the same 'Ignorant Helper' paradigm as in the first experiment, in this case however, our method is based on the study conducted by Gomez and Teixidor (1992; discussed also in Gomez 2004) using only one adult orang-utan (Dona) housed in a zoo cage. This nonverbal task was originally developed to assess Dona's ability to understand knowledge/ignorance of her human partner in a cooperative communicative situation.

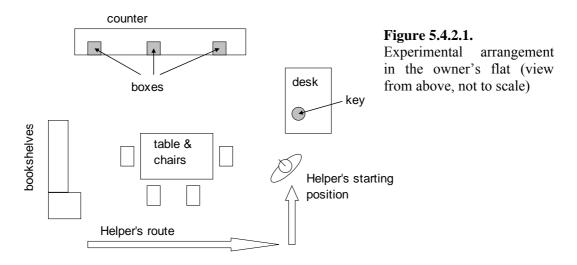
METHODS

Subject

The subject was the same dog who participated in the "Do as I do" study (Study IV – see above); a castrated male Belgian Tervueren, Philip, who was three years old at the time of the experiment (see Experiment IV/1, Methods section for more details). It is important to note that Philip can be regarded as "highly enculturated" individual being an extensively socialized and trained assistance dog for his disabled owner who routinely monitors the state of his owner's attention and uses human behavioural cues in order to effectively cooperate in interactive situations. Therefore Philip can be seen as specially prepared for studying "mind-reading" abilities.

Experimental procedures

We conducted the observations in the living room of the owner's flat (6m x 5m, see Figure 5.4.2.1), which was familiar to Philip. Three boxes (that may be closed by a key) were put on a counter at the height of the dog's eyes at 0.8 m apart from each other. These boxes served to hide the dog's favourite toy (tennis ball). Two persons participated in the experiment: the experimenter (Hider, J.T.) who hid the reward and the owner (Helper) who helped the dog to get the ball. All visits were recorded on video and the training and test trials were analysed subsequently.



Preliminary training

In the first phase of the experiment the dog was trained to solve a simple requesting task. At the beginning of each training trial the Hider entered the room and attracted verbally the dog's attention ("Philip, listen!") with a tennis ball in his hand. Then he went to the desk (the standard place of the key) and picked up the key. After this the Helper slowly approached one of the three boxes, opened it by the key and put in the ball. Having locked the box he placed back the key on the desk and left the room. Next the owner (Helper) entered the room at a predetermined point looking at the boxes he stopped and waited for Philip to approach one of the boxes and to prickle the box with his muzzle. In this situation the owner was allowed to encourage Philip with the "Show it!" command. If the dog did not choose a box then the command was repeated at five seconds intervals, until Philip approached one of the boxes. When the dog indicated one of the boxes unambiguously the owner went to the desk, picked up the key and opened the box chosen by the dog. If the dog chose the baited box then he received the ball for a short play. If the box was empty the owner was not allowed to open another box. Finally, the Helper relocked the box, placed the key on the desk and left the room.

Preliminary training trials were presented 18 times altogether over the course of four weekly visits (4-5 trials per visit). Baiting locations were randomly determined with the restrictions that the ball was put in each box for the same number of times (6) and never placed more than two times in succession into the same box.

Test trials

Following the preliminary training sessions three experimental conditions were introduced in order to analyse Philip's "requesting/informing" behaviour. Experimental situations were designed so that the Helper's knowledge concerning the whereabouts of the Tool (key) and the Target object (ball) were systematically manipulated in three conditions:

(1) Control condition:

The procedure of this condition was identical to the task the dog had to solve in preliminary training trials. These trials included to reveal whether Philip acquired efficient signalling behaviour in the situation where he had to inform the Helper about the place of the reward only.

(2) Hidden key condition:

The procedure of this condition was identical to the Control condition except, when the Hider had locked the ball in one of the boxes, he did not put back the key to the desk but instead he hid it somewhere in the room. The hidden location of the key was different in each experimental trial. In these trials the Helper had no information about the actual location of the ball and he had no information about the location of the key either.

(3) Relocated key condition:

Prior to the trial both the Hider and the Helper entered the room and the Hider picked up the key from the table. He showed it to Philip and then relocated the key to another part of the room. During this the Helper followed the action and movements of the Hider very closely and care was taken that Philip was clearly attending and following each step of the manipulation. The hiding place of the key was varied from trial to trial (e.g. under the carpet, behind a book on the bookshelves etc.). Then both persons left the room and after some seconds the Hider re-entered. He attracted verbally the dog's attention ("Philip, listen!") with a tennis ball in his hand and went to the key. Next he slowly approached one of the three boxes, opened it by the key and put the ball in it. Having locked the box he replaced the key to its recent location (to the place where he found it) and left the room. From this point the trial continued in the same way as in Control condition.

Behavioural rules for the Helper during the test trials

In order to standardize the Helper's behaviour across conditions, he had to act according to the following instructions: After entering the Helper had to go to the "starting point" (see Figure 5.4.2.1) where he was waiting for the dog's signalling behaviour. Once the dog indicated one of the boxes (i.e. he touched one of the boxes or only approached a box within 10 cm-s with his nose and waited there for at least 3 seconds) the Helper had to act differently according to the particular type of trial:

Control.

The Helper picked up the key from the desk and opened the box chosen by the dog. If the ball was there he initialised a short fetching game with the dog.

Hidden key.

The Helper approached the usual place of the key (desk) and started to look for the key for 5 seconds. Then he turned towards the dog and he was waiting for the dog's further actions. If the dog indicated at any time any particular place in the room (approaching, sniffing, prickling with its muzzle, staring) the Helper went there to take a close look. If he found the key he picked it up and opened the box shown by the dog. If no box was indicated, the Helper went back to the starting point and kept on waiting.

Relocated key.

The Helper went to the actual place of the key (to where he put it together with the Hider) and opened the box selected by the dog. If the ball was there he initialised a short fetching game with the dog. The Helper was allowed to open only one box and if the box selected by the dog was empty or they did not manage to get the ball within 1 minute, the trial was terminated and the Helper left the room. The test trials were conducted over 11 weekly sessions, each condition was presented once in each session in a randomised order (3x11 = 33 trials in total). The box in which the ball was put by the Hider was also randomised across conditions. Video recordings of 3 sessions were excluded from further analysis because the owner (Helper) violated the behaviour instructions described above.

Data collection and analysis

The behaviour of the dog was observed during the 1 minute long trials and the analysis focused on the dog's 'indicative' behaviours towards the predetermined directions (i.e. baited box, location of the key). These behaviours were as follows:

Approach: The dog orients towards one of the predetermined locations (key or bait) and approaches it within 30 cm.

Touching: The dog prickles the baited box or the key with his muzzle. On the basis of head orientation of the dog two behaviour variables were recorded:

Gaze alternation: Gazing (head orientation) at the Helper is directly followed (within 2 seconds) by a direct head orientation at the location of the baited box or the key or vice versa. We recorded how many times Philip oriented at the relevant directions (Helper, location of the key, baited box), and how many times he displayed gaze alternation (i.e. back and forth alternation between the three important directions). (For a more detailed description and justification of this kind of behavioural analysis in dogs see Miklósi et al. 2000)

Gazing sequence: For the analysis of the sequence of head orientations toward the three different directions (Helper, baited box, location of the key) we established their relative rank order by noting the order of the directions to which Philip oriented after the Helper arrived at the starting position. Reliability of measuring the number of approaches and touches and the direction of gazing were assessed by means of parallel coding of total sample by two observers. The inter-observer agreements (Cohen's kappa) were 0.92 (approach), 1 (touching) and 0.87 in the case of dogs' orientation.

RESULTS & DISCUSSION

Training for the request task

In the course of the preliminary training trials Philip mastered the requesting behaviour very quickly. He showed the Helper the baited box by approaching and touching it within one minute and the human could select the baited box in all but two trials (88% correct choices).

Test trials

In the test trials Philip showed good performance in all conditions. He got quickly the ball in all (8-8) trials of the 'Control' and the 'Relocated key' conditions (on average within 20 seconds) by utilizing the cooperative behaviour of the Helper. He found the ball in most of the 'Hidden key' condition trials (6 out of 8). It is important to note that in this latter condition for the successful problem solving the dog had to inform the Helper (and at the same time the Helper had to read the dog's behaviour) about both the actually baited box and location of the key. The comparison of problem solving latency (i.e. how quickly the dog got the ball) showed significant differences among experimental conditions. Philip got the ball by the help of the Helper significantly later in the 'Hidden key' condition (Friedman ANOVA, $chi^2(2) = 11.2$; p = 0.003; Figure 5.4.2.2).

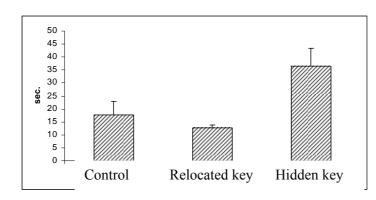


Figure 5.4.2.2.
Latency (mean + SE) of getting the ball in the different conditions. (The time elapsed from starting the trial until the Helper opened the baited box).

We found that Philip indicated the location of the ball by approaching and touching the baited box in all trials of the 'Control' and 'Relocated key' conditions. In contrast, the dog in these conditions approached and touched the key only in 3 cases (out of 2x8 trials). Philip picked up the key and gave it to the Helper before approaching and touching the baited box during the 1st and 2nd trial in the 'Control' and during the 2nd trial in the 'Relocated key' conditions. Importantly, however, dog's signalling behaviour has changed in the 'Hidden key' condition. Philip informed the Helper about the location of the key in most of the trials (6/8). In four cases (3rd, 5th, 7th and 8th trials) he approached the key before going to the baited box, that is, while the Helper were still waiting motionless and in the remaining two cases (1st and 6th trial) Philip first approached and touched the baited box and showed the key only when the Helper failed to find it in the usual location.

Next we analysed how Philip divided his attention between the three particular directions (the Helper, the baited box, the place of the key) in the different conditions. In the 'Control' and the 'Relocated key' conditions Philip predominantly looked at the baited box and the Helper (in sum 84.4% and 85.3% of the total time respectively) and he gazed only rarely at other directions. Interestingly however, in those trials in which the Helper was ignorant regarding the whereabouts of the key ('Hidden key' condition), the pattern of Philip's head orientation has changed

strikingly. He gazed less at the Helper and the baited box (64.5% of the total time) and at the same time he focused his attention towards the location of the key (26.2% of the total time vs. 4% shown in 'Control' and 7% in 'Relocated key' conditions; Friedman ANOVA, $chi^2(2) = 6.4$; p = 0.039).

Next we studied the changes in Philip's communicative behaviour as a function of the Helper's knowledge regarding the whereabouts of the key by analysing frequency of gaze-alternations. Results show that Philip turned his head towards the location of the key approximately two times more frequently when the Helper was ignorant about the place of the key (*'Hidden key'* condition) than in those trials when the key was at its usual location or the Helper was involved in the relocation of the key ($\sinh^2(2) = 9.5$; p = 0.008). Similarly, compared to other conditions Philip performed significantly more gaze alternations between the location of the key and the Helper in the *'Hidden key'* condition ($\sinh^2(2) = 7.05$; p = 0.029).

Moreover alternating head-orientations between the baited box and the location of the key were also observed in the 'Hidden key' condition, but not in case of the other two ones ($chi^2(2) = 10$; p = 0.006). Figure 5.4.2.3 indicates differences in the total number of per-minute gaze alternations across the three experimental conditions; in 'Hidden key' condition Philip alternated his gaze more frequently among the three distinctive directions ($chi^2(2) = 7.46$; p = 0.023).

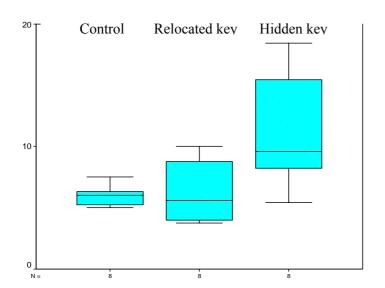


Figure 5.4.2.3.

The total number of gaze alternations (per minute) occurring between any two of the three distinctive directions (Helper, baited box, location of the key) in the three different conditions (median, quartiles and extremes).

We have also analysed the gazing sequence and found characteristic differences between the 'Relocated key' and 'Hidden key' conditions (Figure 5.4.2.4). In the 'Relocated key' condition when the Helper was knowledgeable regarding the whereabouts of the key Philip first indicated the baited box in all but one cases (in the third trial he showed first the location of the key); this was followed by gazing at the Helper and last (if at all) he turned towards the actual location of the key (comparisons of the ranks: $chi^2(2) = 10.75$, p = 0.0024). In contrast, when the Helper had no information about the actual location of both the key and the reward ('Hidden key' condition) we did not find such bias in order of head orientations ($chi^2(2) = 0.75$, p = NS). In this case the location of the key and the baited box was equally preferred to be gazed at as Philip started with looking towards the key in half of the trials (1^{st} , 4^{th} , 6^{th} , and 7^{th}) whilst he indicated first the baited box in the other four cases.

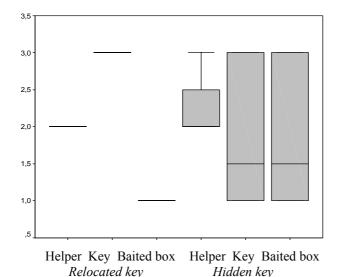


Figure 5.4.2.4.

Rank orders of head orientations (first, second or third direction of looking after the beginning of the trial) in either of the three distinctive directions (Helper, Baited box, location of the key). Median, quartiles and extremes are indicated.

These results show that similarly to that of reported in the case of the orangutan, Dona (Gomez & Teixidor 1992), Philip had no problem with the request task and he could show relevant "pointing behaviour" from the very beginning of the baseline training. Moreover, in spite of the dogs' restricted gesturing abilities Philip modified his behaviour adequately to the different experimental conditions. Philip effectively cooperated with the Helper throughout the tasks because he showed relevant changes in his orienting behaviour and in the frequency of gaze alternations between the target places as a function of Helper's participation in relocating the key. Philip's seemed to have adapted his behaviour to the changes in the Helper's state of knowledge, similarly as observed in the great apes (Gomez & Teixidor 1992; Whiten 2000).

However, compared to Dona's indicative behaviours in the crucial 'Hidden key' condition when the Helper was ignorant regarding the whereabouts of the key (see Gomez, 2004 for a more recent discussion) Philip's performance differed markedly. Namely, whereas the dog approached the key before going to the baited box during the first 'Hidden key' trial and he behaved the same way during 3 additional trials (out of 8), in the first six repetitions of the 'Hidden key' trials Dona pointed to the location of the key after the Helper tried to find it in the usual place (except for the first trial, when she did not indicate the location of the key). After these six repeated trials, however, Dona developed relevant signalling behaviour. Authors concluded that Dona's pointing to the key was not a reaction to human's ignorance ("mental state") but a result of a fast and efficient associative learning.

In accordance with this suggestion we may also assume that a rapid learning process can explain the changes in Philip's behaviour, and as a result he became capable of adjusting his behaviour to the different changed context of the problem situations. So, taking a parsimoniously low-level approach, we can say that discrimination learning is a plausible explanation for the observed behaviour. Some observations, however, seem to contradict this hypothesis. First, Philip met the test situations very rarely (one trial with each condition per week) and the total number of trials (including preliminary training and all testing conditions) was relatively low (51) compared to the several hundreds of trials in Gomez and Teixidor's (1992) study with Dona. Second, over the three months period of the study we could not observe any trends of the changes in Philip's behaviour. So if he had in fact learnt

behavioural strategies for solving problems, it should have been based on very rapid, "insightful" learning.

Although *in situ* learning might have contributed to his performance, the rapid adaptation to the social situation from the beginning suggests that he had already possessed most of the necessary social skills before coming to the experimental situation. This could be explained by his extensive experience with such social situations during his life as an assistant dog but the facilitating role of certain specific skills rooted in the adaptation process of dogs in general could not be ruled out at this stage.

5.4.3. STUDY IX. GENERAL DISCUSSION

The 'Ignorant Helper' design (Gomez 1996b; Whiten 2000) is a useful method for studying sensitivity toward other's presence or absence in past relevant events in both nonhuman animals and in human subjects. Subjects' ability to recognize what the Helper had perceptual access to should be manifested in the adjustment of signalling the place of the Target object and the Tool across the experimental conditions. Among others Whiten (1997) argued that the manifestation of such "mind-reading" skills could be species specific and are displayed as a special kind of behavioural and situational reading ability. Importantly, understanding such overt mental states in others can be developed without any insightful recognition of other's subjective mind-states.

Since this behaviour of both the dogs and the children can be interpreted at different levels, we should make a clear distinction between the "blindly" associationist explanations and the hypotheses inferring theory-based causally interpretive use of relevant perceptual cues (Gergely & Csibra 1997).

'Arousal' Hypothesis

First, it can be argued that the subjects gestured and/or vocalized more and/or alternated their gaze more often in the 'Ignorant Helper' trials because the Helper had left the subject alone in the room with the Hider, which could be more arousing for the subjects. This argument, however, cannot explain why these more frequent gestures, vocalizations and gazes were so specific, often restricted to only the object that the Helper had not witnessed being hidden.

'Discriminative cue' hypothesis

A second possible explanation is that the Helper provided discriminative cues in conditions in which she/he was ignorant of the whereabouts of the toy (for example was looking at the subject more attentively) and dogs (and children) gradually learned to recognize these cues as asking for information of the place of the toy. Two arguments are against it. First, the procedures of both experiments were carefully designed not to allow the Helper to give any feedback to the subjects on what particular information (place of the Target object and/or place of the Tool) she needed. Second, even if the Helper gave unconscious cues to ask for information it is quite unlikely that these subtle cues could indicate to the subjects what particular information (place of the Target Object and/or Tool) the Helper needed. Consequently it seems reasonable to conclude that the subjects' indicating behaviour was influenced specifically by the Helper's previous participation in hiding the objects and not by discriminative cues given by the Helper while passively waiting for the subject's signalling behaviour.

'Specific experiences' hypothesis

However, it is still possible to use the partner's overt, observable features of her participation or disinvolvement as "past discriminative cues" without any understanding of what others have or have not had perceptual access to. In this case, the subject could come to discriminate the relevant conjunction of stimulus preconditions (Helper present/absent) and to use them to form her signalling behaviour discovering the correlation between Helper's presence/ absence and her knowledgeable/ignorant behaviour. Thus it is possible that over the course of their life-long experiences with humans, subjects learned to use the absence of the owner/mother in the close past when a desirable object was getting out of reach of them as a discriminative cue that informs them that they are needed to indicate the place of this object more intensively. If we assume some understanding of the Helper's participation/involvement which goes beyond using specific cues only, the question remains as to whether this understanding is limited to representing the behaviour of the Helper or based on understanding the casual connection between participating and knowing. What do the subjects take into account? Do they tailor their indicating behaviour directly to the Helper's involvement or absence in relevant past events or to the Helper's knowledge or ignorance inferring from her past participation?

'Disinvolvement-ignorance-informing' hypothesis

If the subjects are able to attribute knowledge and ignorance to their partners, and they are ready to react in an active, initiating and complementary way, then they are expected to provide the information which the partner's ignorance requires. This interpretation implies the ability to understand the casual connection between seeing and knowing as has been observed in three-year-old children (e.g. Wimmer et al. 1998; O'Neill et al. 1992) as opposed to the previous three and the next non-mentalistic explanations.

'Disinvolvement-informing' hypothesis

There is, however, a lower lever explanation that relies on a direct relationship between the Helper's participation vs. disinvolvement in certain past events and his/her predicted behaviour without an intervening variable (Whiten 1996) of a mental state attributed to his/her. When interpreting the results that 2.5-year-old children tailored their toy-signalling behaviour to the previous visual access of the parent to the hiding of the toy, O'Neill (1996) suggested that "2-year old children tailored their communication by, first, taking into account the parent's disengagement from the events taking place and, second, by wanting to update the parent about the relevant events that happened while the parent was disengaged" (O'Neill 1996, p. 673). This ability "may have rested not on a sophisticated, casual understanding of knowledge and its relation to sensory experiences but, rather, on a simpler, precursory understanding of the form "Tell other people about significant happenings they did not take part in with me". (p. 674). Based on this argumentation the "disinvolvement-informing" hypothesis may explain the children's (and dogs') capability for adjusting to others previous perceptual access.

Finally, we should note that despite the surface similarities the cognitive mechanisms underlying such performance in dogs and children may rest on different processes. Nevertheless these findings provide further support for the dogs' improved social competence suggesting that dogs (like children), having been raised in socially enriched human environment, may be able to generalize their own past experiences in order to predict other's behaviour as well as to recognize that a particular sequence of events and/or actions precede certain behaviour response (and specific changes in mental states) in others.

5.5. CONSTRUCTING COMMUNICATION: SUMMARY OF RESULTS

Social cognition as the capacity to process socially relevant information is an essential component of the dog cognitive equipment that allows this domestic animal to communicate and interact with humans. However, the enormous variations of human social behaviour and diversity in human communication often enough challenge the dog's capacity to understand others. 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 initialising and maintaining communication (e.g., eye-contact) and rely on various behavioural cues for recognizing attention. An intriguing question is, 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. In this chapter we have provided some evidence that this pattern of behaviour can be revealed in situations where dogs are exposed to insoluble problems in the presence of humans (STUDY IX). Under these circumstances, dogs show many forms of behaviour (gazing, gaze alternation, vocalization) that direct the attention of the human onto themselves or the problem to be solved (see also Miklósi et al. 2000; Gaunet 2008; 2010). Comparative experiments have shown that this behaviour 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 (see STUDY I. for more details), which can in principle provide the basis for the emergence of complex communicative interactions between humans and dogs in situations like the request task in the 'Ignorant Helper' method (STUDY IX).

(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 behavioural cues of human attention in dogs. Dogs have a robust ability to share attention with humans; they are very skilful in using human gaze in object-choice situations in which dogs both follow and direct human gaze (for a review see Kaminski 2009). Recent research has also provided clear indications that dogs are sensitive to the direction of human visual attention in various contexts; e.g. when they beg (Gácsi et al. 2004), perform forbidden actions (Call et al. 2003) or asked to fetch an object (Kaminski et al. 2009a).

Moreover increasing evidence suggest that domestic dogs show early (Riedel et al. 2008; see also STUDY VI) and somewhat infant-like (STUDY VIII) sensitivity to cues that signal the human's communicative intent (eye contact, verbal addressing). It seems that dogs use eye-contact and directed talk provided by humans to infer whether they are addressed in a particular situation (STUDY VI /Exp. 1) and like infants, they can discriminate intended communicative acts and non-communicative goal-directed behaviours (STUDY VI /Exp. 2).

(3) Responsiveness to human communicative gestures.

Recently, intensive research efforts have revealed that dogs can rely on various human bodily gestures as communicative referential signals. In these experiments dogs have to find hidden food based on cues provided by a human (for a review see Miklósi & Soproni 2006). Dogs can use various forms of pointing (e.g., Hare et al. 1998; Soproni et al. 2002) 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 later can also rely on pointing cues after intensive socialization and some training (Virányi et al. 2008 but see 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).

In addition, other experiments have shown that some dogs tend 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). The special importance of human manipulation even against other (non-social) discriminative cues is further supported by the results of STUDY VII and STUDY VIII showing that dogs preferably rely on human-given cues in two-way object choice tasks and this bias can lead to "efficiency blindness" in social learning situations. Dogs can make inference by exclusion, this reasoning however, is manifested in their performance only in that case when choice from among the two target places can not be made on the basis of social-communicative cues (directional gestures, eve contact, gaze shift – STUDY VII/ Exp. 1 & 2). Assessing the relative importance of social-communicative cues versus attention-catching effect of non-social discriminative stimuli we also found that dogs, like 18-month-old infants, show "efficiency blindness" in an observational learning situation depending on the ostensive-communicative signals from human demonstrator and the presence of the demonstrator during their choice(STUDY VII/ Exp. 3).

Further results of comparative experiments point to a novel aspect of dogs' and human infants' perseverative search bias: the role of ostensive-communicative signals in the emergence of A-not-B error (STUDY VIII). Our findings show that these errors reflect the subjects' susceptibility to the human communicative cues embedded in the search task. It seems that human-reared wolves are unable to develop a similar sensitivity to human communicative signals. This functionally infant-analogue manifestation of social competence in dogs supports the hypothesis that caninization in the human environment have preferred traits for which the cues of human communication are relevant and important concomitants of the social environment.

Finally, it should be mentioned that the emergence of behaviours such as gaze alternation between an inaccessible target and a human, apparent attention-getting signals (e.g. vocalization) and the influence of the physical presence and/or the attentional status of a human on the propensity to exhibit these communicative signals (see also Miklósi et al., 2000; Gaunet 2008; 2010) support the view that dogs meet many of the operational criteria (see Leavens et al. 2005) for the initiation and maintenance referential and intentional communication with their human partners.

(4) "Mind-reading" skills.

Further observations on dog communication with humans suggest that they might be able to complement information that is missing in the human (STUDY IX). The experiments presented in STUDY IX are the first ones which systematically

tested and compared children and dogs as to whether each is able to tailor their signalling behaviour to a human's past participation/disengagement by understanding the social situation with especial regard to the contribution of the human partner in the manipulative actions. Results show that in spite of the dogs' restricted gesturing abilities subjects, at least in some situations, modified their behaviour 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 behavioural cues indicating the lack of certain "knowledge".

Dogs' sensitivity to past perceptual access of humans is in line with earlier studies (Call et al. 2003; Gácsi et al. 2004 and STUDY VI), that have demonstrated in different situations, that dogs can recognise what a human can or cannot perceive (see) at present. This sensitivity of dogs can provide the grounds for tailoring their behaviour to the past perceptual access of others (for further corroborating evidence see Cooper et al. 2003).

In summary, the results presented in this chapter seem to confirm the hypothesis that dogs are evolutionary prepared to learn to use signals of the human non-verbal communication to interpret human action and they may also used these cues to extrapolate information from human behaviour. All this suggests that independently from the actual underlying mental mechanisms dogs display analogue functioning in terms of performance to preverbal infants in ostensive-communicative situations. At the same time, although dogs seemingly understand the communicatory nature of different interspecific (i.e. dog-human) social interactions, this does not mean necessarily that they represent and learn any about the mental state of the human or understand that others perform acts intentionally (with a goal in mind).

CHAPTER 6

PUTTING THINGS TOGETHER: A GENERAL FRAMEWORK FOR STUDYING SOCIAL COGNITION IN DOGS

6.1. CHARACTERIZATION OF DOG'S SOCIAL COMPETENCE

Dogs undeniably possess a wide variety of social-communication skills. A puzzling feature of these skills is that these often manifest in a sophisticated manner in interspecific interactions (toward people) whereas dogs do not seem to utilize the very same skills in dog-dog (intra-specific) interactions. A good example for this strange variance is the use of gaze cues. Whereas dogs apparently tend to establish eye contact with humans and readily utilize human gaze cues in different collaborative situations (see the above studies for more details), they rely on this means of communication restrictedly in intraspecies interactions (Bradshaw & Nott 1995).

It is increasingly accepted that the key to the puzzle of dogs' "inter-specific" social competence is the fact that the human social environment provides a natural niche for dogs (see Chapter 2). The dogs' ancestors encountered a human-dominated environment that was specifically challenging for them by virtue of its complex social and cognitive nature. Therefore, as a consequence of the shared environment, many social skills in dogs have undergone convergent evolutionary changes, and many aspects of dog behaviour have become functionally analogue counterparts to the corresponding human trait. Following this line of argument, it becomes evident that the parallel investigation of dog (versus wolf) and human (versus chimpanzee) behaviour may be beneficial for our understanding of the evolutionary processes.

In comparative work, however, the actual performance of the dogs should be compared in terms of the range of environmental and social factors and intrinsic constraining abilities (see enculturation issue below for more details). In the case of socio-cognitive abilities we suggest that such performance should be described in the framework of social competence. Social competence of an individual can be interpreted as the functional manifestation of an array of skills that allows it to conform to the changing challenges of its social environment. As abilities comprising social competence have been under divergent selection pressure in different species, one may expect that each species possesses skills that function within a certain range of social and environmental factors and differ in their complexity. The task for comparative research, therefore, is to find those aspects of social competence that are different or shared in dogs, wolves, children and nonhuman ape species.

In the last few years different ideas have been proposed regarding the typical characteristics of social competence in dogs as well as the key differences between dogs versus apes and dogs versus wolves. Note that these ideas are not necessarily exclusive but could provide a useful basis for systematizing findings and testing particular experimental hypotheses.

6.1.1. Social dog – causal ape

The "social dog versus causal ape" hypothesis was coined by Bräuer et al. (2006) who suggested specific differences between great apes and dogs in the ability to make inferences from cues of different types as to the location of hidden food.

Accordingly, this hypothesis infers specific differences in the social competence of dogs and apes claiming that dogs have evolved inter-specific social sensitivity including preference for a wide range of cues of human ostensive and referential communication. This "infant-like" sensitivity (see Chapter 5 for more details) enables them to interpret human behavioural signals better than their non-domesticated ancestors and better than the human's closest relative.

In one set of experiments Bräuer et al. (2006) compared dogs' and apes' performance in two way object choice tasks in which subjects were required to find a hidden food on the basis of either non-social cues representing physical causal association (e.g. noise made by the hidden food) or social-communicative signals referring to the location of the food (e.g. pointing from a greater distance). Dogs, unlike chimpanzees, were especially skilful at reading human communicative behaviours whilst they showed little success in understanding physical causal relations. In contrast, chimpanzees outperformed dogs in understanding causal relations in the non-communicative versions of the object choice task. These findings support previous findings that great apes face problems in reading some human social cues, e.g. they typically perform at chance in situations in which a human informs the subject by communicative gestures (e.g. Herrmann et al. 2007, but see Okamoto-Barth et al. 2008). Importantly, it seems that reinforcement history in regard to using human gestures is of less importance for dogs because puppies as young as six weeks utilized human gestural cues for finding hidden food (Riedel et al. 2008, but see Udell & Wynne 2010).

6.1.2. Cooperative dog – competitive ape

A modified version of this account, which can be labelled as "cooperative dog versus competitive ape" (Hare & Tomasello 2005) hypothesis, suggests that the key difference between dogs' and apes' social competence is that domestication enhanced the development of special skills in dogs, which can be utilized especially in those situations in which a human communicates in a cooperative manner (e.g. providing informative cues and or imperative orders – see STUDY VIII). So whereas dogs follow cooperatively ("voluntarily") human gestures independently of the target referred by the signal (see STUDY VII), chimpanzees show "utilitarian" use of their (human) partner's signals. Increasing evidence suggests that apes routinely interpret their partners' acts (gazing, reaching etc.) as an indication of selfish intention to obtain a target (e.g. Bräuer et al. 2006; 2007; Okamoto-Barth et al. 2007) but have difficulties understanding the human's informative (altruistic) motive (e.g. Povinelli et al. 1990). Whereas already 12-14 month old human infants comprehended communicative intentions in the object choice task (e.g. Behne et al. 2005), adult chimpanzees are seemingly unable (or unwilling) to select the referent successfully if it has no relevance for them. The fact that dogs and chimpanzees differ specifically in their use of human communication in object choice situations may lend further support to the hypothesis that dogs, unlike chimpanzees, have been specifically selected for engaging in cooperative activities with humans. This view suggests that the contexts in which partners share information about resources by providing communicative signals do not fit with the cognitive mindset of chimpanzees, whose social competence manifests more adequately in competitive situations.

6.1.3. Evolutionary enculturated dog – wild wolf

A third approach addresses wolf-dog differences in particular with regards to the functional manifestation of social competence in these species. The complex hetero-specific communicative abilities of dogs in comparison with wolves can be regarded as the outcome of specific evolutionary changes in the social cognitive mechanisms (see Hare et al. 2002) or non-specific associative conditioning (Udell et al. 2008). Evidently, it is unlikely that the relatively short evolution of dogs has produced fundamental changes in the cognitive machinery so there is no reason to suppose the existence of an innate ability to "understand" human signals in the total absence of individual experience. However, without denying the importance of learning (Udell et al. 2009) and individual socialization (c.f. enculturation - Chapter 2.4), we may suppose the existence of evolutionary (i.e. genetic) predispositions in dogs, which facilitate the emergence of heterospecific communicative interaction with people.

It should also be noted that the genetic contribution to any particular "social-cognitive" trait (measured in an experiment) may be small, and additionally, the effects of genes on such complex epiphenomena as social cognitive skills are likely to manifest through interaction with environmental factors. That is, genes influencing the emergence of cognitive skills in dogs may not do so directly, but rather indirectly, by making individuals more sensitive to the effects of certain environmental factors. Importantly, such small (and often interactional) effects can be easily overlooked if one varies environmental influences when comparing dogs to wolves. Keeping this point in mind, our studies (see STUDY I, STUDY II) compared the behaviour of hand-raised dogs and wolf puppies under identical conditions to reveal early species-specific differences that could be attributed to the effect of domestication (see also Miklósi et al. 2003; Virányi et al. 2008; Gácsi et al. 2009).

This "gene-environment interaction" approach suggests that wolves with particular social experience may also show evidence for social-communicative skills (e.g., flexibility to detect human visual cues of attention – Udell et al., 2011; utilizing human pointing gesture – Gácsi et al. 2009), and the dogs' social competence is also affected by the age, rearing conditions, and treatment practices. Interestingly, we may draw a parallel between dogs and human children with regard to the studies comparing "socially deprived" (shelter/orphanage) individuals with typically developed samples (pet dogs/children in families). For example, it has been recently reported that many children who have resided in very deprived institutional environments may exhibit specific deficits in cognitive and social functioning (Rutter et al. 2007). This autistic-type behaviour pattern is an acquired syndrome that may be related to institutionalisation. Thus, the environment can have a significant effect on human social cognition.

Note this hypothetical example: Providing evidence that enculturated (human-reared) chimpanzees outperform children with institutional autism (e.g., in a task based on the subject's ability to follow human's gaze) should not lead one to conclude that human-specific genetic predispositions, which may have evolved during hominization, play no role in gaze following behaviour in particular or in the manifestation of other aspects of human social cognition. In a similar vein, one cannot reject the possibility that a genetic predisposition (domestication effect) exists in the dog on the basis of the finding that dogs with limited human social experience often show poor spontaneous sensitivity to human signals, while intensely trained

and socialised wolves perform reliably under certain conditions (see e.g., Udell et al., 2011).

6.1.4. A synergetic model of the emergence of dogs' social cognitive skills

In line with the approach focusing on the genotype-by-environment interaction we propose a model of the general effects of domestication that takes into account both genetic and environmental variability in the dog and wolf, as well as the fact that the same developmental endpoint (performance in a particular task) can be achieved through different pathways. This account differs from the linear gene—phenotype approach by positing a causal role for neither genes nor environment in isolation, but for their synergetic co-participation in the emergence of social cognitive skills, where the effect of one is conditional on the other.

This synergetic model (Figure 6.1.4.1) presumes that there was some positive selection for genetic factors during domestication, some of which play a role in sociality (e.g. von Holdt et al. 2010), especially with respect to heterospecific interactions. This could include preference towards humans, looking at human gaze, and so forth. These changes allow for social experience during development to have markedly different effects on the behaviour of dogs and wolves. The most important aspect of this model is that in dogs, the effects of positive selection (genetic advantages) manifest only in a proper social environment, and even without such selective history, wolves can also reach high levels of interspecific social skills if socialised intensively.

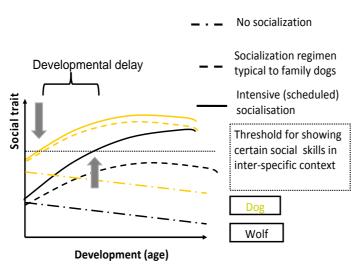


Figure 6.1.4.1. A simple sketch of the synergetic model on the emergence of interspecific social skills in dogs and wolves. model assumes genetic advantage on the part of the dog for acquiring a range of social skills that are utilised in the human-dog relationships. These social skills emerge after relatively short social experience with humans. Wolves can also develop comparable social skills; however, they need significantly more intensive human social input to approach

or achieve the same levels of performance. Lack or intermission of social experience may lead to deteriorated social performance in both species, but this process is faster in wolves.

Furthermore, there could have been several points in the development of the two species when, depending on the differential genetic and social environmental contributions, no difference between dogs and wolves would have been observed with regard to social skills. It is important to note that socialisation or social experience should be regarded as maintaining environmental stimulation, in the sense of Caro and Bateson's (1986) model on behavioural development; thus, harmful social experience or intermissions of social experience may disrupt the manifestation of former social skills. In our view, species—environment interaction seems a

particularly suitable approach for understanding the development of social cognition in both dogs and wolves, because this epiphenomenon is known to be associated with environmentally mediated factors, yet individual dogs and wolves display considerable heterogeneity in their response to those environmental exposures.

The synergetic model makes several predictions for which there is general support. First, it predicts that dogs need less social experience with humans and less scheduled (i.e., more "ad hoc") social experience with humans than do wolves to achieve the same level of social skills. It seems that dogs have a head-start in being attentive to humans and in responding to human-given cues correctly (Riedel et al. 2008; Gácsi et al. 2009; see also STUDY 1). Second, dogs without or with little interspecific social experience show retarded social skills that may be actually inferior to those observed in socialised wolves (Udell et al. 2010), and third, the model predicts that intensive socialisation, as compared to the "customary" socialisation, will have a smaller performance-improving effect on dogs' social skills in comparison to wolves.

In conclusion, the effects of domestication on the social skills of dogs should be evaluated in a framework of more flexible behavioural models that consider the contributions of genetic and social factors.

6.2. THE INFANT-LIKE CHARACTER OF THE DOGS' SOCIAL COMPETENCE

In line with the aforementioned theoretical considerations (Chapter 2) and on the basis of the experimental findings presented in Chapters 3-5 we propose that the social competence in dogs has been affected by the challenges of the human social environment. As a consequence of these adaptation requirements (i)dogs have evolved some special skills for interacting with and communicating with human beings, (ii)these skills provide the basis for fast (and efficient) social learning about human communicative behaviours in dogs and (iii)contribute to a more "infant-like" and less "wolf-like" functioning of social cognition in this species. In fact, recent observations have revealed interesting parallels between dogs' and human infants' tendency to participate in communicative interactions with humans and to gain knowledge through social/observational learning

6.2.1. The interactive nature of human communication and its role in efficient social learning

When speculating about hominine evolution, it is often assumed that the adaptational demand manifesting in the necessity of making fast and efficient sharing of intentions and emotions and generic knowledge among group-mates was the crucial driving factor (Gergely et al. 2007). In line with this assumption it has been proposed that a highly specialized social learning system was one of the basic cognitive adaptations that evolved in response to this evolutionary challenge. In the long run this evolutionary innovation has paved the way for the emergence of culture in the increasingly closed and individualized groups of the *homo* line.

The crucial point of this evolutionary leap was that, during hominization, the communication became such an interactive mechanism that was characterized by two human-specific features. First, it enabled transfer of (cultural) knowledge in a uniquely fast and efficient manner between the companions even if the knowledge to

be acquired is cognitively opaque (that is, the recipient is limited in gaining insight about the causal structure/means-ends relationships of the manifested knowledge). Second, this mechanism ensured that naïve social learners acquire knowledge which is generalizable across contexts even after one or few observations (see Csibra & Gergely 2009 for a recent review).

The significance of this evolutionary innovation lies in the fact that transmission of generic knowledge between individuals via non-human types of social/observational learning is a very slow and fortuitous process. In fact, the knowledge manifested by a "demonstrator" in a social learning situation is always episodic: the recipient becomes informed about objects and/or events that are relevant only to the particular context of "here-and-now". The acquisition of nut cracking in wild chimpanzees (Boesch et al. 1994), for example, clearly demonstrates the limitation of social learning without being supported by the aforementioned human-like interactive communication mechanism because the learning process is time consuming and it takes about 3–7 years for the infant chimpanzee to master the skill (Inoue-Nakamura & Matsuzawa 1997, but see Mashall-Pescini & Whiten 2008)

The artificial world of humans has been far more challenging than the social and physical environment of chimpanzees. Human abilities for using and constructing complex tools as well as social structures made our world extremely complex, in which the cultural knowledge to be transmitted is often "opaque" regarding its aim as well as the cause-effect relationships. Therefore early humans must have faced serious problems at the emergence of material culture during the hominine evolution. Csibra and Gergely have recently hypothesized (2009) that a new type of communicative learning system, natural pedagogy, may have emerged as an evolutionary solution to this social-environmental challenge in order to facilitate the transmission of more complex knowledge more rapidly.

Increasing evidence suggests that this communicative learning system is present in early infancy and utilizes infants' special sensitivity for ostensive-referential demonstrations of knowledge (see Study VIII for more details). That is, during this interactive process, in addition to the *manifestation of the knowledge* to be transmitted (e.g. splitting the nut by stone), the "teacher" uses signals *expressing his/her communicative intent* and directional/referential signals *to specify the referent* (i.e. what (s)he is informing about). For the observer, at the same time, the ostensive referential communication serves to highlight the relevant, generalizable aspects of the knowledge and provides an effective guide even though the naïve learner (e.g. preverbal infant) has no clear understanding of causal relationships and cannot gain insight into the hidden cognitive processes of the "teacher". Thus natural pedagogy creates a shortcut for the novice by getting around that long and cognitively demanding process during which the observer first has to understand the causal structure and cognitive background in order to acquire generalizable knowledge.

6.2.2. The dog: infant mind in wolves' clothing?

Importantly, human social settings provide a wide variety of cognitively demanding (opaque) inputs not only for young infants but also for dogs, whose social learning skills have been presumably adapted to the complex human social environment (see above). Our studies provide corroborating evidence that similarly to preverbal human infants, dogs fulfil at least two out of three operational criteria for being a recipient in "pedagogical" knowledge transfer (see Chapter 5).

First, dogs show special sensitivity to such ostensive cues that signal the human's communicative intention and they also show some evidence of the recognition of information transferring nature of communicative contexts. Like in infants, ostensive-communicative cues guide the dogs' attention and influence their inferences and interpretations in object search tasks (STUDIES V, VII & VIII). They also show differential sensitivity to human gaze-shift in communicative context as compared to a non-communicative situation and ostensive-communicative addressing signals facilitate gaze-following behaviour in dogs (STUDY VI).

Second, dogs seem to comprehend the referential character of human cuing in a way similar to human infants (see STUDY VI for more details). These results suggest that human ostensive-communicative referential signals trigger an attentive, "ready-to-learn" (and/or "ready-to-obey") attitude in the dog which makes the dog capable of remarkably adepting at learning from humans.

Third, an important consequence of this receptive learning attitude is that dogs are willing to reproduce those cognitively "opaque" actions that they have seen in a communicative referential context even if the action is unusual, or represents a counter-productive solution to the problem. The emergence of "efficiency blindness" (or selective responsiveness) in observational learning situations (STUDIES VII & VIII), which depends to a large degree on the ostensive-communicative-referential aspect of the situation, is a typical manifestation of this "ready-to-obey" attitude.

All of these findings raise the possibility that dogs may understand some aspects of human communicative motives, and, for the dog, the function of human demonstration is probably not knowledge transfer *per se* but facilitating the performance of those behaviour actions which lead to effective behavioural synchronization in order to avoid conflicts in the group and/or to co-act in terms of common actions without necessarily comprehending the causal structure of the collaborative interaction. Such a disposition prepares dogs (as well as young infants) to efficiently learn from humans in a wide range of situations. From an evolutionary perspective, this trait paved the way for the emergence of complex and variable cooperation between dogs and humans leading to a wide variety of shared social competences between domestic dogs and young preverbal human infants.

In summary, we think that the theoretical and experimental analysis of the Dog Behaviour Complex in comparison with the Human Behaviour 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.

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