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**Comparative social cognition: behavioural, genetic and
neurohormonal components**

Doctoral thesis

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“We are, by nature, a highly affiliative species craving social contact. When social experience becomes a source of anxiety rather than a source of comfort, we have lost something fundamental — whatever we call it”

(Insel 2002)

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Introduction

The vast majority of animals (all that reproduce sexually) live at least partly in social environments and social behaviours thus constitute a crucial part of their lives. The study of social behaviour goes back thousands of years (Székely et al. 2010), and interest in the topic has even increased in recent years. A reason for this might be the fact that social competence (Taborsky & Oliveira 2012), is widely believed to be a key to answering the question “*what makes us human?*”

There is a common agreement that human social cognition can indeed be considered special and that one of the key elements during human evolution was a change in social behaviour. However, there are several different proposals regarding what exactly is special about human social behaviour. One of the widely accepted proposals (Tomasello et al. 2005) states that shared intentionality – the ability to participate in collaborative activities with shared goals and intentions – is the crucial difference between human and non-human cognition. The proposal is based on the argument that such activities require not only especially powerful forms of intention reading and cultural learning, but also a unique motivation to share psychological states with others and unique forms of cognitive representation for doing so. Although the authors of this proposal undoubtedly argue that the question of human–primate differences is complex (Tomasello et al. 2003) – e.g. it cannot be simply stated that the difference lies in that humans have a theory of mind and chimpanzee do not –, one of the main critics against this and other proposals is that they focus on the prominent role of one key social skill in human evolution, such as shared intentionality (Tomasello et al. 2005) or pedagogical receptivity (Csibra & Gergely 2009). In contrast, Csányi (2000) suggested that there is more than one social skill that played a role during hominization and that instead of the arbitrary selection of one major characteristic all these important human traits need to be analyzed together as a behaviour system. In other words this proposal claims that after the *Pan-Homo* split, instead of one major change a series of small changes occurred in human behaviour that affected a wide range of social features. Thus it is suggested that a single causal chain of changes cannot explain the evolution of complex social behaviour in humans as previously proposed, but instead it needs to be considered as a “mosaic evolution” of several skills.

Despite the above outlined open theoretical questions and contrasting (or complementary) proposals the common agreement stands that human social cognition can, in one way or another, be considered special. Although there were some early attempts in comparative psychology trying to prove that human social behaviour is not different from that of other species (e.g. enculturated apes were also shown to comprehend human language similarly to human children – Savage-Rumbaugh et al. 1993), from an ethological viewpoint it is to be expected that humans possess special behavioural skills (in the domain of social cognition or as a matter of fact in any other domains). It is long known that all animal species have something special not only in their morphology, but also in their behaviour that differentiates them from other species, thus it is not at all surprising that there are certain elements of human behaviour that are not found in other species. Oskar Heinroth (1910; cited in Podos 1994) was the first to suggest within the framework of avian taxonomy that the methods of comparative morphology can be applied to behaviour as well. This suggestion was based on the observation that

members of different species can be reliably distinguished based on their characteristic behavioural patterns. However obvious this statement might seem to us now, its importance lies in the fact that it shifts our attention from the question of “*is the behaviour of a given species special?*” to the question of “*in what is the behaviour of that species special?*” Needless to say that from an anthropocentric point of view – that is undeniably one of the main motivations behind most comparative research – it is considerably more interesting to find out how we humans differ from the rest of the animal kingdom, compared to finding out how two goose species differ from each other, thus our more specific question in this case is “*in what is human behaviour special?*”.

Research aiming to unravel social skills that are uniquely human has identified several behavioural elements that differentiate us from other species. It has been suggested that human social cognition is strongly connected to the exceeding number of individuals that constitute human society and its concomitant complexity. It is undoubtedly an important element of human evolution that group size has increased conspicuously resulting in behavioural changes such as decreased within-group aggression and increased cooperation (Csányi 2003). However, if group size was considered as the sole measure of complexity, then humans would not be the unanimous pinnacle of sociality as ultra-social colonial insects also approach (or even exceed) the group size of human societies. The crucial difference lies in that while invertebrate colonies are constituted by genetically identical or at most closely related individuals, human social complexity is based on quite different principles (Richerson & Boyd 1998). The “Human Behaviour Complex” (Csányi 2000) provides a multifactorial framework for those skills that are supposed to have played a crucial role during human evolution and thus resulted in uniquely human social behaviours. The model identifies three interrelated behavioural dimensions: (i) social traits connected to group life (e.g. group loyalty, xenophobia, complementary cooperation), (ii) behaviour mechanisms for synchronization of activities (e.g. rule following, empathy, imitation) and (iii) constructive abilities (e.g. abstraction, mimics, language use). It is assumed that the sum of small evolutionary changes in these behavioural dimensions, that emerged in response to environmental challenges in the social domain, are responsible for a qualitative difference in human sociality compared to any other social system.

Biological background of human social behaviour

Another line of research aiming to understand the evolution and/or uniqueness of human social behaviour combines the study of different organisational levels (e.g. genetic background, neural mechanisms) and recent studies are indeed providing substantial insights into the biological background of human sociality (Skuse & Gallagher 2009). Several different approaches exist within this framework, among which the most prominent hypothesizes that it is the neurohormone oxytocin that had the most permissive role in the evolution of the human nervous system (Carter 2014). It is even suggested within this framework that *Homo sapiens* could not have evolved without the neurohormone oxytocin as the success of this species highly depends on social behaviour and cognition.

Oxytocin – which undoubtedly plays a central role in the expression of the high levels of sociality that are essential to contemporary human behaviour (Carter 2014) – is in evolutionary terms a remarkably conservative nonapeptide, that plays a particularly prominent role in the modulation of social life across mammalian taxa (Yamasue et al. 2012). This neurohormone for

example has been shown to regulate social contact (Bales & Carter 2003), pair bonding (Insel & Shapiro 1992), maintenance of monogamous relationships (Scheele et al. 2012) and parental care (Olazábal & Young 2006). More importantly for the above presented approach, increasing body of evidence supports the notion that oxytocin is specifically involved in the regulation of human social cognition (Lee et al. 2009). However, although there is a general agreement on the prosocial effects of oxytocin, there are various arguments about how these are mediated and the differences between viewpoints are often implicit rather than clearly delineated (Campbell 2010). Much of the debate focuses on methodological issues about which are the low level (e.g. cellular) mechanisms behind the oxytocin effects, how results of different studies can be compared and which details of the procedures are important and should thus be carefully controlled for (Guastella et al. 2013). Our current knowledge of the behavioural effects of oxytocin in humans is mainly based on three mostly independent approaches: (i) correlational studies measuring oxytocin in the periphery (urine, saliva, blood) or in the CSF, (ii) gene \times behaviour association studies involving receptor (OXTR) polymorphisms, and (iii) experimental studies manipulating (both the peripheral and CNS) levels of oxytocin using intravenous or intranasal administration (for an evaluation of these approaches regarding their informative value in terms of the underlying central nervous mechanisms see: Heinrichs et al. 2009). The following is a short summary of the involvement of the oxytocin system in regulating human social behaviour.

In the first study that investigated the relationship between oxytocin and human social cognition (Heinrichs et al. 2003) it was found that oxytocin enhances the buffering effect of social support on stress responsiveness in a psychosocial laboratory stress protocol. Participants who received both protective factors of social support (from their best friend) and oxytocin showed significantly attenuated cortisol and behavioural stress responses compared with participants who received social support combined with placebo or no social support. Similarly, later studies have found that oxytocin reduces fear responses to social stimuli (Kirsch et al. 2005) and it was also revealed that the mechanism behind this effect is the attenuation of amygdala activation (Domes et al. 2007b). Several related studies followed these findings and proved that oxytocin acts on multiple levels of human social cognition by encouraging social approach, affiliation and complex social phenomena, such as trust (Kosfeld et al. 2005; Baumgartner et al. 2008) or generosity (Zak et al. 2007; Barraza et al. 2011).

Another increasingly popular line of research investigates the effect of oxytocin on several aspects of face processing. Faces play a strikingly important role in human social interactions as they convey vital information about the interactants' identity as well as their mental and emotional states (gender, age, familiarity, intention etc.). It has been revealed by several recent studies that face perception (or at least some aspects of it) is also mediated by the neurohormone oxytocin; for example it increases gaze to the eye region of human faces (Guastella et al. 2008a; Andari et al. 2010) as well as it increases perceived facial attractiveness and trustworthiness (Theodoridou et al. 2009; Kis et al. 2013). Oxytocin has also been shown to enhance facial perception and recognition in humans (Savaskan et al. 2008; Rimmele et al. 2009) as well as to improve emotion recognition from faces (Domes et al. 2007a). More specifically, this latter study for example investigated the effects of oxytocin on the ability to infer the affective state of another individual from facial cues by giving participants a set of

pictures showing the eye region of emotional faces, and asking them to infer the internal state of the depicted person. A single intranasal dose of 24 IU oxytocin enhanced performance in this test compared to placebo, leading the authors to conclude that oxytocin improves the ability to infer the mental state of others. Somewhat in line with these results Guastella et al. (2008b) also reported positive effects of intranasal oxytocin on adult male humans' social memory. In their study human faces showing happy, angry or neutral expressions were presented to participants who received either intranasal oxytocin or placebo. It was found that on the following day participants who had been given oxytocin provided more “remember” responses when the faces were previously seen with a happy, rather than an angry or neutral expression.

It should be noted, however, that there are a variety of confounding factors and additional components that contribute to the regulation of human social behaviour. For example, the peripheral increase of oxytocin in lactating women has been associated with dampened levels of adrenocorticotrophic hormone (ACTH; Chiodera & Salvarani 1991) and cortisol (Amico et al. 1994). There is also evidence that the oxytocin system is in some way regulated by gonadal steroids as the human oxytocin promoters are activated by estradiol (Richard & Zingg 1990), most probably through an indirect mechanism. These results indicate that similarly to the above detailed multifactorial approach explaining the evolution of human social cognition, the underlying mechanisms also constitute a complex system that cannot be explained by one single characteristic.

Models of human social behaviour¹

A crucial question in studying human social behaviour – as well as its biological background – in a comparative framework is what species to compare to. Most of the recent discussion about different animal models is in the clinical field (e.g. McGonigle 2014; Stewart & Kalueff 2014), but the question is also important in basic comparative research. Several different species have been used as models of human social behaviour in a comparative framework, and they all can be best used to answer different types of research questions. In the following I will briefly outline the advantages and limitations of the most widely used animal models.

Laboratory rodents (mice and rats) are the “classical” and most widely used model species. A big advantage of these rodent models is that they are relatively easy to keep under laboratory conditions, and that due to the existence of standardized test protocols results obtained in different studies can easily be compared. These experimental protocols include such long-used and well-established tests as for example the social isolation paradigm – that models the effects of social deprivation – when subjects are kept on their own for a certain time period in a given age and the effects of this treatment on different aspects of social behaviour are studied (see e.g. Hol et al. 1999); or the resident-intruder test – commonly used to elicit aggressive behaviour – when an animal is introduced in the cage of a territorial conspecific (see e.g. Raab

¹ This chapter is partly based on: **Kis, A., Miklósi Á., & Topál J. (2013).** Dog, human, chimpanzee: Comparative analysis of animal communication from a cognitive perspective (Kutya, ember, csimpánz: Kognitív szempontok a fajok kommunikációs eltéréseinek értelmezésében) *General Linguistic Studies (Általános Nyelvészeti Tanulmányok)* (ed. Csaba Pléh; Akadémiai Kiadó) XXV. 173–192 (in Hungarian); **Topál, J., Kis, A., & Oláh, K. (2014).** Dogs' sensitivity to human ostensive cues: a unique adaptation? *The Social Dog: cognition and behavior* (eds. Kaminski, J. & Marshall, S.; Elsevier), in press DOI:10.1016/B978-0-12-407818-5.00012-7

et al. 1986). Furthermore as laboratory rodents are extensively studied many information has already been accumulated about them for example as models of autism (Narita et al. 2010), abnormal aggression (Haller 2013), or social stress (Blanchard et al. 2001). Laboratory rodents have also long been used to study the underlying physiological mechanisms of social behaviour, and a considerable proportion of novel techniques (e.g. gene knockout: when one of an organism's genes is made inoperative – e.g. Winslow et al. 2000; optogenetics: a technique to control and monitor the activities of individual neurons – e.g. Deisseroth 2011) have been developed and successfully applied for these species. On the other hand, a common critique against laboratory rodents is that the model systems used are artificial (e.g. the different conditions under investigation are artificially induced in the laboratory, while in case of humans these are naturally occurring behaviours; e.g. Overall 2000). A further danger is that the translation of behavioural and neurological findings from rodent studies to humans bears the risk of drawing oversimplified parallels (Heinrichs & Domes 2008). Nevertheless, the findings of this approach have long been and are still providing valuable information that could not be obtained from other model systems, especially about the underlying mechanisms of social behaviour.

Although we have seen that drawing direct parallels between the mechanisms behind human social behaviour and that of species as remotely related as rodents is already a problematic issue, with a slight change of focus research on phylogenetically distant taxa can be very informative for understanding the evolution of human social behaviour. This line of research – instead of trying to understand a phenomena in the model species and then speculating about whether the same mechanisms are responsible for the parallel human behaviour – investigates behaviours that are already well-studied in humans in phylogenetically distant species. This way the aim of this approach is to unravel which are the evolutionary precursors of certain human social behaviours. One of the most widely studied phenomena within this framework is social learning, and research in this field has found that a wide variety of taxa – including a turtle (*Pseudemys nelsoni*; Davis & Burghardt 2011) and a tortoise (*Geochelone carbonaria*; Wilkinson et al. 2010a) species, fish (*Toxotes jaculatrix*; Schuster et al. 2006) and the common octopus (*Octopus vulgaris*; Fiorito & Scotto 1992) – is capable of social learning and thus acquiring new information via the observation of conspecifics instead of costly trial and error learning. Social learning is of course only vaguely defined in this context as the tasks used and the capabilities demonstrated in the different species vary greatly with the common ground being the acquiring of new information with the help of observing another individual. Other research topics within this framework include collective decision making in three-spine stickleback (*Gasterosteus aculeatus*; Ward et al. 2008), personality in firebugs (*Pyrrhocoris apterus*; Gyuris et al. 2011), or maze navigation by the plasmodium (*Physarum polycephalum*; Nakagaki et al. 2000). While the capacities in all these cases are only remotely similar to the human behavioural skills, this line of research is useful in highlighting that some basic behavioural mechanisms exist that are adaptive for and wide-spread across phylogenetically distant species. Obviously the handful of studies that have been conducted studying each of these social skills is not nearly enough to unravel the exact nature of these common mechanisms, but further research in this framework could lead us to the evolutionary ancient origins of human social cognition.

Another “classical” line of research compares the behaviour of humans to their phylogenetically closest relatives, the primates. The logic behind this approach is similar to the above outlined, namely that if it is found that humans share certain social skills with other primate species, then it is an argument for the presence of that skill in the common ancestor. The common ancestor is of course much less remote in this case compared to the investigation of phylogenetically distant taxa, and perhaps even more importantly in this case differences between humans and non-human primates can shed light on uniquely human behavioural skills. The picture gets more complicated when in the latter case we intend to decide for or against evolutionary continuity arguing that the differences are only quantitative or that they are major qualitative differences (see e.g. Savage-Rumbaugh et al. 1993 & Burling et al. 1993 for both of these arguments in the context of language use in apes). It seems from research conducted within this framework that human social cognitive functioning is biased for a prosocial attitude which is in contrast with the typical behavioural patterns of other apes (Hare et al. 2000, 2001). Based on this line of research it has been suggested that this cooperative, prosocial bias may have been one of the key factors that made it possible for humans to develop higher-level cognitive skills (Richerson & Boyd 1998; Moll & Tomasello 2007). This line of research has also revealed, on the other hand, several similarities in the social behaviour of human and non-human primates. This includes for example the ability to follow a human experimenter’s gaze – a social skill that allows individuals to take advantage of the visual experience of others – that is present in both chimpanzee (*Pan troglodytes*) and rhesus macaques (*Macaca mulata*) from the (respective late- or early-) infant ages on (Tomasello et al. 2001). Aversion to inequity, a fundamental skill for prosocial behaviours and cooperation also seems to be present in some of the great ape species (Brosnan 2011), e.g. in chimpanzee (*Pan troglodytes*) and bonobos (*Pan paniscus*), although not in others, e.g. orangutans (*Pongo pygmaeus*)– as demonstrated in an exchange based task where subjects could either complete the task or not and could either accept the reward the experimenter offered them or not.

As we have seen many studies following the above described phylogenetical approach have reported not only similarities, but also specific differences between social behaviour of humans and other primates (Herrmann et al. 2007). These findings suggest that in order to fully understand the evolution of human social cognition the ecological and social environments during post-*erectus* human evolution as well as relating selective pressures also need to be considered in these comparative investigations. In fact humans’ closest phylogenetical relatives, the great apes are not only separated from humans by 6 million years of evolution but they also live in and are thus adapted to considerably different ecological niches. Each of these niches that a species occupies presents different social problems and different levels of social complexity. This means that the socio-cognitive abilities of these species have also been formed by specific adaptational demands. Another line of research takes advantage of this evolutionary process of adaptation to certain environments and aims to detect phenotypic convergence in species that live in the same environment and are thus adapted to similar environmental challenges. Humans share their natural environment with several other species that, during the process of domestication, have presumably adapted to the same niche and are thus facing similar challenges in their social environment (Miklósi et al. 2007). This line of research received much attention when it turned out that domestic dogs (*Canis familiaris*) are

able to follow human momentary distal pointing gestures in order to locate hidden food (Soproni et al. 2002; Miklósi et al. 2004). To utilize this challenging form of pointing gestures flexibly, dogs must infer something about the communicative-referential meaning of the human's gestures. Dogs' high performance in these tasks is surprising because even our nearest primate relatives, the great apes, fail at it (Hare et al. 2002; Kirchhofer et al. 2012), as do wolves (*Canis lupus*; Hare et al. 2002; Miklósi et al. 2003). Later on research has confirmed dogs' human-like social skills (Miklósi et al. 2004; Hare & Tomasello 2005) in many other tasks as well and thus dogs became a widely used convergent model species of human behaviour (Topál et al. 2009a). Several elements of the "Human Behaviour Complex" (Csányi 2000; see above) have been successfully studied in dogs (Miklósi et al. 2007) and the research of dog behaviour, evolution and cognition has grown to be a field on its own right (Miklósi 2007).

General aims

The aim of the present thesis is to combine different (although far not all) approaches of comparative social cognition and present how each of them may help us understand human social behaviour. First, different animal models (a phylogenetically distant reptile and phylogenetically closely related primate species as well as two domestic species adapted to the human environment) will be presented illustrating how they can be used to answer several sub-questions of this indeed very broad topic (*Parts I-III.*). Next, the underlying genetical and neurohormonal mechanisms of certain aspects of social behaviour will be studied, focusing on the oxytocin system in domestic dogs (*Part IV.*). Finally, the connection between comparative social cognition research and applied science will be outlined, presenting an example of its use in social robotics (*Part V.*).

PART I: Social skills shared with an evolutionarily ancient taxon²

As outlined in the Introduction, one of the most basic questions of comparative social cognition is to find out which are the capacities that humans share with other taxa, and which are the ones that are unique to humans. It is now known that basic social behaviours and the precursors of complex human social behaviours can be found in evolutionarily distant taxa (Wilkinson & Huber 2012), thus comparing the social skills of species with relatively simple social behaviour to that of humans is an increasingly popular approach.

Background

Learning from the observation of others was long thought to be a distinctive characteristic of humans; it was even suggested that a more appropriate name for the human species would be *Homo imitans*, man who imitates (Meltzoff 1988). Imitation is considered to be the pinnacle of social learning and the basis of cultural transmission (Heyes et al. 2009). There is now evidence that non-human mammals (Subiaul et al. 2004) and birds (Klein & Zentall 2003) are also capable of imitation; however we know nothing about these abilities of the third amniotic class – reptiles.

Reptiles and mammals all evolved from a common amniotic ancestor and investigation of similarities and differences in their behaviour is essential for understanding the evolution of cognition (Doody et al. 2012). Recent advances in the field of reptile cognition have found evidence of sophisticated abilities in this group. The red-footed tortoise (*Chelonoidis* – formerly *Geochelone* – *carbonaria*) is capable of gaze following (Wilkinson et al. 2010a) and can learn to solve an otherwise insolvable task by observing the actions of a conspecific (Wilkinson et al. 2010b). Furthermore, the Florida redbelly turtle (*Pseudemys nelsoni*) is able to learn to approach a visual object cue by observing conspecifics that had learned the task (Davis & Burghardt 2011). Though these findings provide evidence that reptiles can use social information, the mechanisms that control their behaviour remain unclear.

The present study used a bidirectional control procedure (Dawson & Foss 1965) to investigate whether bearded dragons (*Pogona vitticeps*) are capable of imitating a conspecific. This task was designed to control for both social influences and emulation/enhancement effects when testing imitation. The paradigm involves comparing the performance of two groups of observers watching demonstrations that differ in their body movements but create identical (or symmetrical) changes in the environment. Imitation occurs when subjects perform the demonstrated action more often than the alternative action.

Methods

Subjects

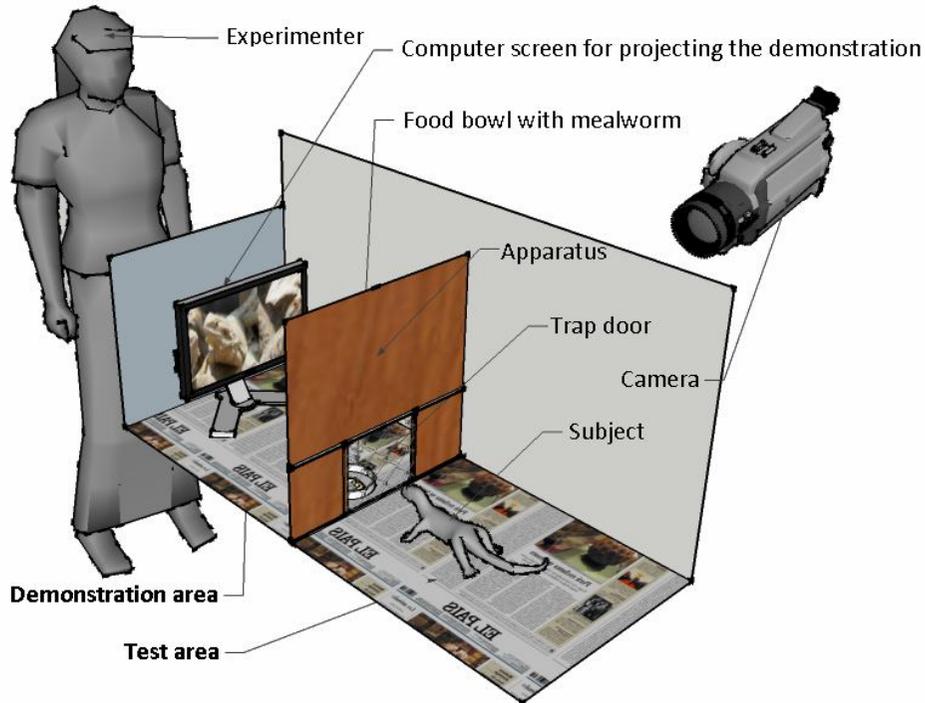
The bearded dragons either belonged to the Small Animal Unit at the University of Lincoln (N=7) or were privately owned (N=6) but were kept at the university throughout the study. Our subjects were 5 males and 7 females (within the age-range of 1-3 years). All animals were handled by humans on a daily basis. In order to avoid that male subjects respond aggressively

² This chapter is based on: **Kis, A., Huber, L., & Wilkinson, A. (in prep.)** Social learning by imitation in bearded dragons (*Pogona vitticeps*)

to the video demonstration, the demonstrator we used was a 3 year old female. (Females are often housed together and show no aggression towards each other.)

Experimental arrangement

Testing was carried out in an experimental arena (100cm×40cm×50cm) that was divided by the test apparatus into two equal parts: the test area (where the subjects were located) and the demonstration area (where the computer screen was positioned). The test apparatus itself was a 40cm×40cm wooden board with a 12cm×12cm hole. This was covered by a wire door which could be moved along sliding rails in either a leftward or a rightward direction (Figure 1).



1. figure Test setup

Procedure

All subjects were habituated to the experimental arena before the onset of the experiment. They were considered habituated when they readily explored and ate mealworms placed in a Petri dish (used later as a reward in the test trials) in the experimental arena. During this time they were not exposed to the apparatus used in the test.

The subjects received two trials a day separated by a break. Each trial started with a short (30 sec) habituation phase when the experimenter placed the subjects in the experimental arena and they were allowed to explore freely. This was followed by the demonstration phase, when an 11 second video was presented via a computer monitor. In the two experimental groups the demonstration showed a conspecific approaching the test apparatus, opening the door rightwards (or leftwards) and going through it. To ensure that the lizards learned about the behaviour of the conspecific and not a simple rule of moving the door towards (or away from) a salient part of the apparatus (Heyes 1994), the demonstrator was trained to open the door in one direction (right) and the stimulus video was flipped for presentation of the leftward opening. In the control group the demonstration showed a conspecific standing in front of the apparatus and

the door opening by itself to the right side. None of the videos showed the demonstrator being rewarded. One of the videos projected for demonstration (right side opening) can be found at: <http://www.cmdbase.org/web/guest/play/-/videoplayer/231>

Following the demonstration a white plastic board was placed in front of the lizard whilst the test apparatus was placed in the arena (this took approximately 5 seconds). Afterwards the subjects were allowed free access to the test apparatus and their behaviour was recorded for 5 minutes. The trials were terminated and the subjects were returned to their home enclosures if they successfully opened the sliding door to any side and went through it or if the 5 minutes were over. If subjects were not able to get to the mealworm (by opening the sliding door to any side and getting through it), they were not rewarded, even if they opened the sliding door.

Behavioural coding and analysis

In all trials we coded the side to which subjects opened the door with: +1 for left, -1 for right and 0 for no opening. In those rare cases (6 out of 120 trials) when a subject opened the door to both sides in the same trial it received both scores +1 and -1 (=0). Opening was defined as a visible gap at either side of the door. Behavioural coding was blind to experimental condition and the inter-observer reliability (based on double coding of 20% of the test trials – 2 trials / subject) was high ($\kappa=0.92$). The side of opening on the first successful trial (when the first opening occurred) was compared to 50% chance level using a Binomial test (data of the two experimental groups was pulled together). Opening score (reflecting the sum of all ten trials) was compared to the chance level of 0 by using a Wilcoxon Test (data of the two experimental groups was pulled together). The three groups were compared by Kruskal-Wallis test (followed by pair wise Mann-Whitney post-hoc tests). The correlation between the number of successful experimental subjects in a given trial and the number of previous trials administered was assessed in order to check for the effect of repeated exposure to the task (Kendall's tau). Furthermore the number of successful experimental subjects was compared within a daily session between the first (trials 1, 3, 5, 7, 9) and second (trials 2, 4, 6, 8, 10) trials administered on that day (Wilcoxon test).

Results and Discussion

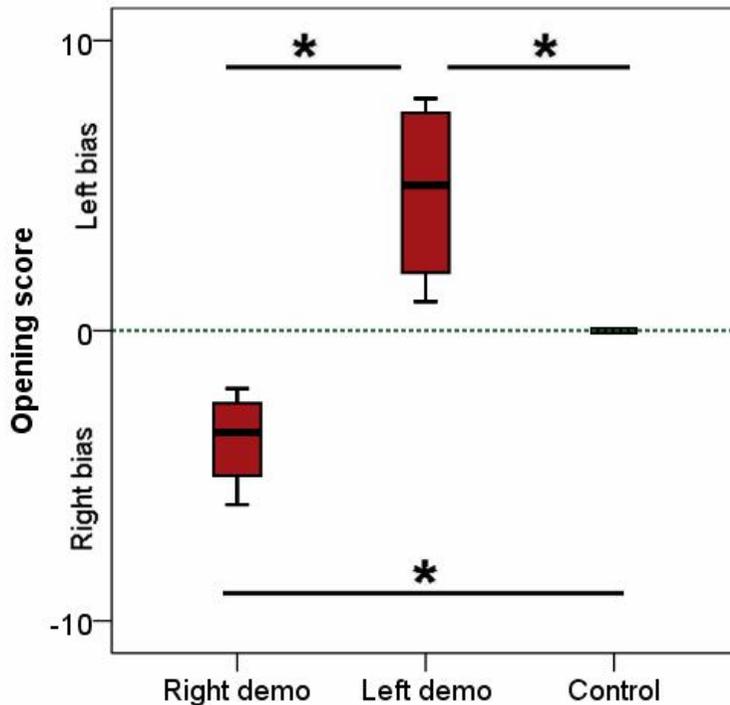
All experimental subjects successfully opened the sliding door whereas none of the control subjects did. Furthermore, on their first successful trial all 8 experimental subjects opened the door to the side that they had observed the demonstrator opening (Binomial test, $p=0.008$). This side preference was consistent across the entire experiment with a significant 67-100% bias towards the demonstrated side (Wilcoxon Test, $T+=37$, $p=0.007$). The three groups also differed from each other in the side of opening (Kruskal-Wallis Test, $\chi^2=10.277$, $p=0.006$; Figure 2).

However a considerable individual variation was observed. Of the 8 experimental animals the number of successful openings varied from 2/10 to 10/10 and the first successful opening varied from trial 1 to trial 5.

The number of successful experimental subjects was not related to the number of previous trials administered ($r=-0.025$, $p=0.926$). The number of successful experimental subject in the first and second trial of a daily session did not differ either ($Z=0.141$, $p=0.888$).

These results reveal evidence of imitation in a reptile species and suggest that reptiles may possess the cognitive abilities necessary for cultural transmission. This is not compatible with

the frequently repeated claim that only humans, and to some lesser extent great apes, are able to imitate (Byrne 2003). Rather, our findings indicate the adaptive nature of socially aided learning, which provides a shortcut to finding a solution and avoids the costly process of trial and error learning (Boyd & Richerson 1988). Previous studies have already revealed evidence of social learning in fish (Schuster et al. 2006) and tortoises (Wilkinson et al. 2010b). However, the present study is the first to investigate the role that imitation may play in social learning in reptiles.



2. figure Side preferences for the three groups calculated from the 10 trials. *: $p=0.029$

The fact that our subjects were exposed to multiple trials during the experiment raises the possibility that individual learning also contributed to the performance of bearded dragons; however we could not find any association between the performance of subjects and the number of previously administered trials. Furthermore our results showing that the first successful opening occurred to the demonstrated side indicate that the performance of bearded dragons we observed is due to imitation.

Claiming that a species can learn by imitation depends on how precisely this is defined, as imitative performance can vary according to the copying fidelity and the ‘goals’ of imitation

(intention or outcome) (Heyes & Ray 2002). Nevertheless, the bearded dragons copied the demonstrated action selectively and were unsuccessful in the control condition. This suggests that the social learning shown by this species is not goal emulation but fulfils the criteria of imitation (Zentall 2006). In sum, the present findings suggest that reptiles exhibit complex cognitive behaviour equivalent to that observed in mammals and birds and suggests that learning by imitation is based on ancient mechanisms.

PART II: Phylogenetical approach³

A more “classical” approach aiming to find human-specific social skills and/or precursors of human social cognition compares human behaviour to that of our phylogenetically closest living relatives, the primates (e.g. Savage-Rumbaugh et al. 1993). This approach looks for similarities between humans and non-human primates in certain test situations as an indication for an evolutionarily shared capacity; and for differences between the species as a special human adaptation.

Background

In recent years much attention has been devoted in the field of comparative psychology to a search error originally described by Piaget (1954) that occurs during object permanence tasks. This so-called “A-not-B” error, occurs in infants at the age of 8-12 months when children successfully retrieve a hidden object several times from one of two locations (called “A”) but then fail to change to the other location (“B”) even if the object was placed there in their full view e.g. they perseverate and continue to search in location “A”.

In the infant literature many explanations have been proposed for the “A-not-B” error. According to Gratch et al. (1974) the “A-not-B” error might occur due to the failure of understanding specific properties of the desired object. Deficits of the short-term memory may also lead to the “A-not-B” error (Cummings & Bjork 1983). Sophian & Wellman (1983) argued that the error might arise from the conflict between previous and recent information. Furthermore, Baillargeon et al. (1985) proposed that motor action coordination problems might cause the “A-not-B” error. According to Diamond (1985) this error results from the inability to inhibit previously rewarded action. Finally, Smith et al. (1999) suggested discussing the “A-not-B” error in terms of the repetition of motor schemes.

Recently, in human infants, committing the “A-not-B” error has been explained by the children’s misinterpretation of the communicative hiding game as a kind of teaching session where the repeated, communicative hiding of the object in location “A” conveys information that the goal of the task is to visit this place independently from the actual hiding location of the object (Topál et al. 2008). The general form of this interpretation, the Natural Pedagogy hypothesis, claims that human infants have a high preference for ostensive-communicative signals (e.g. eye-contact) and they are biased to learn semantic or generic information from demonstrations accompanied with such signals (Csibra & Gergely 2006).

Interestingly, object searching tasks have been conducted also with various animal species using the Piagetian categorization (Gómez & Go 2005). In this framework, grey parrots (*Psittacus erithacus*; Pepperberg et al. 1997), domestic dogs (*Canis familiaris*; Topál et al. 2009, but see Gagnon & Doré 1992), Eurasian jays (*Garrulus glandarius*; Zucca et al. 2007) cotton top tamarins (*Saguinus oedipus*; Neiworth et al. 2003), magpies (*Pica pica*; Pollok et al. 2000) and squirrel monkeys (*Saimiri sciureus*; de Blois et al. 1998) have been reported to reach Stage 4 object permanence characterized by the “A-not-B” error. One study on common marmosets by Mendes & Huber (2004) reported that some of their subjects reached the

³ This chapter is based on: **Kis, A., Gácsi, M., Range, F., & Virányi, Z. (2012).** Object permanence in adult common marmosets (*Callithrix jacchus*): not everything is an “A-not-B” error that seems to be one. *Animal Cognition*, **15**, 97–105.

Piagetian Stage 6. However, they also found a huge variation in the performance of different individuals. Regarding the “A-not-B” error in common marmosets, we have no conclusive results since the methods of this study were not designed to test this question. Similarly to most other animal research that study aimed at determining which levels of object permanence the species in focus can reach. Hardly any studies, however, investigated the underlying mechanisms why animals commit the “A-not-B” error (but see Dumas (1992), Gagnon & Doré (1992)).

There are indications that, similarly to human infants, non-human primates also show preferences to gaze cues (Myowa-Yamakoshi 2003) and use face-to-face communication in mother-infant interactions similarly to humans (Ferrari et al. 2009). Obviously though, no non-human primates use eye contact and other communicate cues for teaching as do humans (Caro & Hauser 1992; Csibra 2007). Still, it is possible that the use of eye-contact in animals provides a basis for responding to human-given ostensive-communicative cues, especially if they have extensive experiences with humans. If human ostensive cues function as a kind of supernormal stimuli, the animal’s response on the receptive side may even exceed the range of the natural response typical in within-species contexts. Such responsiveness might explain why chimpanzee babies attend more to a human (making eye contact and talking to the subject) than to their own mother in an object manipulation task (Bard & Vauclair 1984). Most of the object permanence tasks conducted on primates avoided the social cuing of the experimenter (e.g. Neiwirth et al. 2003; Mendes & Huber 2004). Therefore, until now, we have no information about whether, additionally to previous explanations, the Natural Pedagogy hypothesis also applies to primates. In our experiment we directly tested whether experimenter given social cues can induce the “A-not-B” error in marmosets.

Based on their ecology, also common marmosets may have such sensitivity to ostensive-communicative cues. Common marmosets live in family groups with a cooperative breeding system in which all members participate extensively in rearing the offspring (Tardif et al. 1993). The youngsters learn socially about food preferences of older animals (Voelkl et al. 2006) and even food sharing occurs exceptionally often (Feistner & Price 1991; Kasper et al. 2008). It has been shown in manipulative tasks that social learning as well as cooperative problem solving are facilitated by the joint interaction and the relaxed relationship between the animals (Werendich & Huber 2002; Caldwell & Whiten 2003; Dell’Mour et al. 2009). Based on these characteristics one can expect high interest and sensitivity towards others’ behaviour, which has been demonstrated by the firm evidence that common marmosets are capable of imitation (Voelkl & Huber 2000, 2007).

This study takes a mechanistic approach to study the “A-not-B” error in common marmosets. We tested with a 2×2 design whether marmosets commit the “A-not-B” error more often after social-communicative hiding than in a non-social context (which would follow from the Natural Pedagogy hypothesis), and whether their success in the “B”-trials is influenced by the trajectory of the hiding of the target object.

Methods

Subjects

The experiment was carried out on 26 adult marmosets (11 males and 15 females, mean age: 8.44 ± 4.03 years) living in 5 family groups. One animal had to be excluded due to motivational

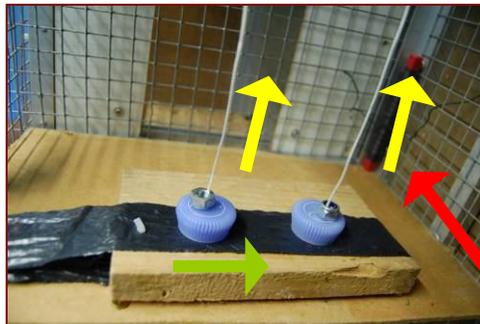
problems. All animals were born in captivity and lived in the research facilities at the University of Vienna (Department of Cognitive Biology) and the Konrad Lorenz Institute for Evolution and Cognition Research (Altenberg).

The families were kept separately in indoor cages of $250 \times 250 \times 250$ cm (in Vienna) and $200 \times 350 \times 300$ cm (in Altenberg), equipped with branches and ropes. The monkeys were fed fruits, vegetables, monkey pellets, and protein supplements; water was continuously available. Before the onset of the experiment all marmosets had participated in other cognitive tasks including the manipulation of boxes to recover food.

Subjects were assigned to two groups, and accordingly they participated either in the *Asymmetric* or the *Symmetric* “A-not-B” test (see *Methods* section). Each marmoset participated in the social as well as the non-social condition in a randomized order.

Apparatus

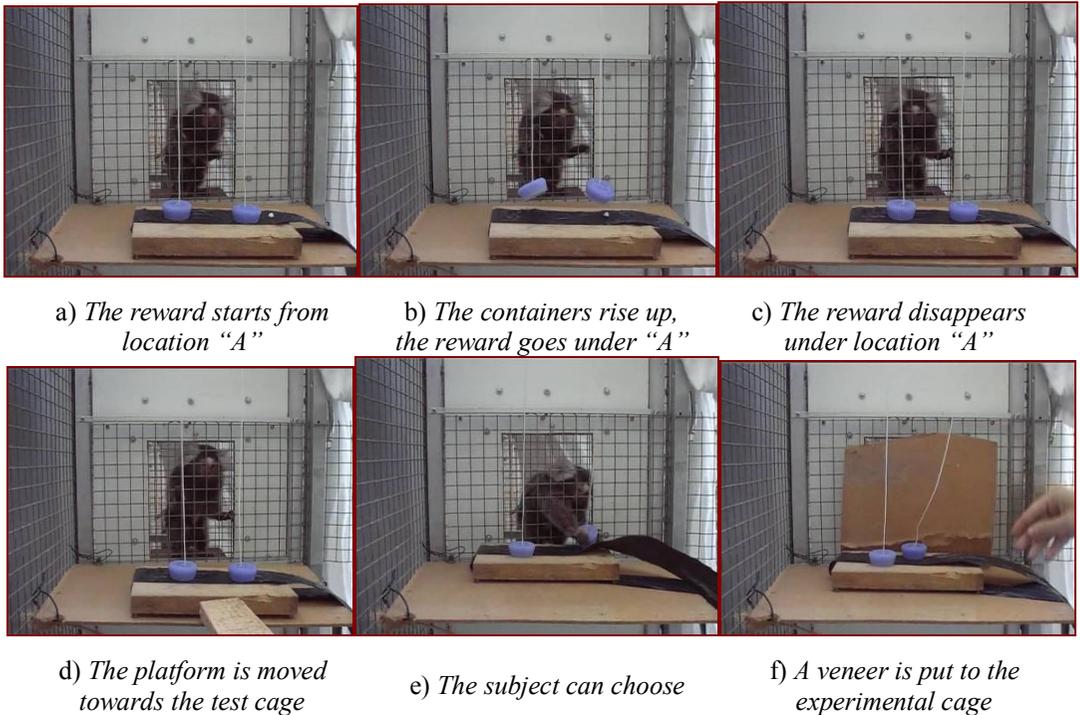
The apparatus (Figure 3) consisted of a wooden platform that could be moved back and forth in front of the experimental cage. Two identical containers were placed on the platform one of which was baited with a piece of coconut. The containers could be moved remotely via pulling on two strings connected to them. A wire mesh separated the subject from the platform. The subject could reach the containers through the mesh when the platform was pushed close. Each marmoset was familiarized with this action in the pre-test when they had to retrieve two times a piece of food from below a single container placed in the middle of the platform.



3. figure The apparatus used in the experiment. The red arrow indicates the moving of the entire platform towards the subjects, the green arrow the moving of the food reward and the yellow arrows the moving of the containers. During the non-social trials the black stripe was used to move the food reward.

General procedure

The experiment was carried out in the same way as in the infant study by (Topál et al. 2008). In four subsequent “A” trials the subject could observe the bait being hidden under the same (“A”) hiding place (for half of the animals it was the right container, for the other half the left container). After each hiding the experimenter allowed the subject to choose one of the two containers by pushing the platform within reach of the animal (Figure 4). If the subject had at least three correct choices out of the four trials we continued with the “B” trials. If the animal did not reach the primary criterion, two additional “A” trials were presented. In the latter case, the criterion was set at four correct choices out of six trials before the “B” trials were administered.



4. figure Non-social A trial. A video protocol can be found at <http://www.cmdbase.org/web/guest/play/-/videoplayer/140>

Asymmetric and symmetric "A-not-B" tests

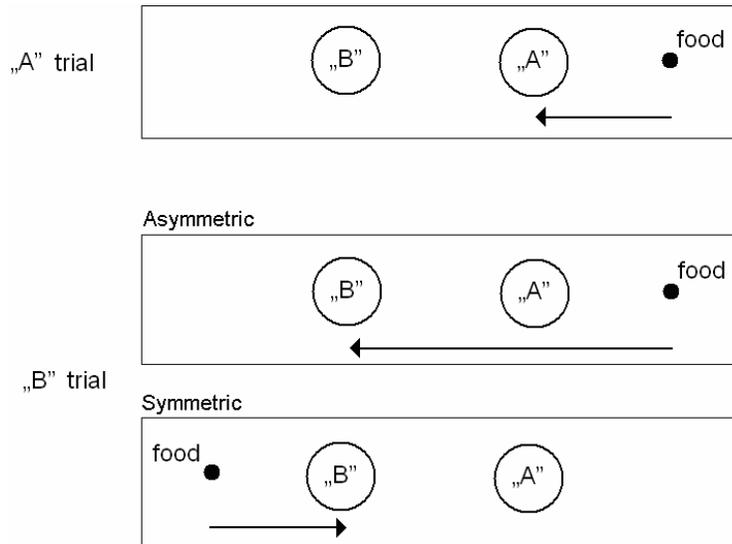
In the asymmetric test trials, the reward always started from the same location next to container "A" on the right/left end of the wooden platform. Accordingly during the "A" trials the reward was moved directly to the adjacent "A" container, but in the B-trials the reward first moved below the "A" container and reached the "B" location only afterwards. The two containers were lifted at the approach of the object and lowered only after the reward reached location B (Figure 5). In the symmetric test the "A"-trials were identical to those of the asymmetric test but in the "B"-trials the reward started from the opposite side of the platform and went directly to the "B" hiding place without moving below the "A" container (Figure 5).

Social and non-social conditions

The moving of the containers and the reward was identical in both conditions but the context of hiding varied in regard to the visibility and the behaviour of the experimenter (E).

In the *non-social* condition, the E stood behind a curtain and hence the subject could not see her. She followed the marmoset's behaviour on the LCD display of a camera that was placed opposite to the subject. Before each hiding, the E waited until the subject came to the wire mesh, then lifted the two containers remotely, and via pulling on a stripe (see Figure 4) she moved the reward to either "A" or "B" location from behind the curtain.

In the *social* condition, the E sat opposite to the subject who could see her face, upper body and hands during the entire test. Before hiding, she called the subject's name and established eye-contact with it. She waited until the subject came to the wire mesh, then lifted the two containers remotely. Then she picked up the reward (that was at the same starting position as in the non-social trials) from the stripe, and following the same path as in the non-social condition e.g. she moved the reward with her hand to location "A" or "B" without pulling on the stripe.



5. figure Hiding trajectory in the different trials

In *both* conditions the manipulations were stopped if the subject did not pay attention, and restarted when the subject oriented again towards the apparatus. After hiding, the E pushed the apparatus into reach of the subject so that it could choose a container. A choice was coded when the subject touched one of the two containers. After a correct choice the subject was allowed to retrieve the reward. If the choice was incorrect, the E immediately put a veneer in front of the mesh separating the subject from the platform (see Figure 4). The next trial was prepared similarly, without the subject seeing it. If the subject did not make a choice within 20 seconds, the hiding was repeated (similarly to Mendes & Huber 2004).

A daily test session for a subject took about 8-12 minutes. All the tests were videotaped for later analysis.

Data analysis

In all of the four test conditions, we coded the number of correct choices separately for the “A” and for the “B” trials. Based on the number of correct choices in the first 4 “A”-trials (performed in the same way in all conditions), we found that neither age (Spearman-correlation: $r=0.1$; $p=0.616$) nor sex (Mann–Whitney-test; $Z=1.263$; $p=0.263$) of the marmosets influenced their performance. Accordingly, we analysed the effect of 3 factors with a Generalised Estimating Equations model (SPSS16 programme): within subject factors: “A” versus “B” trials, social versus non-social situation; between subject factor: asymmetric versus symmetric test. According to the results of this analysis, we compared the number of correct choices to the chance level of 50 % with one-sample Wilcoxon tests (InStat programme).

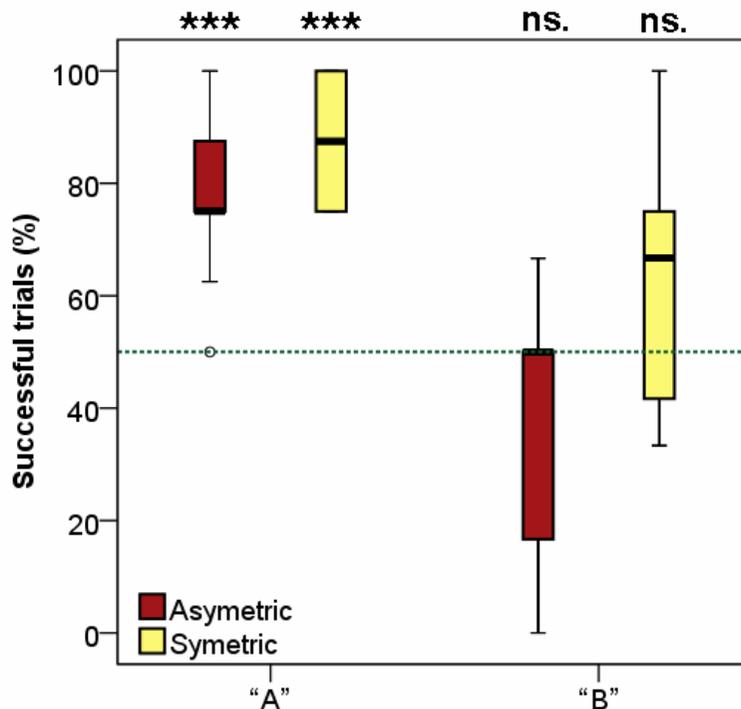
The looking behaviour of the subjects was also coded during and after the hiding event. We compared the *social* and *non-social* conditions with respect to looking at the demonstration (hiding event) and looking at the two hiding places (“A” and “B”) after the hiding (Wilcoxon test).

Results and Discussion

The Generalised Estimating Equations model revealed that both “A” versus “B” trials ($\chi^2=32.487$ $p<0.001$) and asymmetric versus symmetric tests ($\chi^2=8.724$, $p=0.003$) had a

significant effect on the subjects' success while social versus non-social test situation had no significant effect ($\chi^2=0.352$, $p=0.553$). No interactions were found between the factors. Accordingly we pulled together the data from the social and non-social tests.

Both in the asymmetric and symmetric tests subjects performed above chance level in the "A" trials (one-sample Wilcoxon test: $p<0.001$), but the number of successful trials in the "B" trials did not differ from the chance level (asymmetric: $p=0.162$; symmetric: $p=0.137$). This result was supported by the fact that subjects were more successful in the "A" trials than in the "B" trials (Wilcoxon matched-paired test; asymmetric: $Z=4.036$, $p<0.001$; symmetric: $Z=3.001$, $p=0.003$). At the same time, subjects in the asymmetric "B" trials were less successful (made more mistakes) than in the symmetric ones (Mann-Whitney test; $U=166.000$, $p=0.007$) (Figure 6).



6. figure Subjects performance in the different condition. ***: $p<0.001$, ns.: $p>0.05$

Although subjects' performance did not differ in the *social* and in the *non-social* condition, we did find some differences in their looking behaviour. Marmosets were more attentive to the hiding event (looked more at the demonstration) in the *social* compared to the *non-social* condition both during the "A" ($Z=2.381$; $p=0.017$) and during the "B" ($Z=2.819$; $p=0.005$) trials. This was most probably due to the fact that in the *social* condition a human hand moved the hiding places, that resulted more interesting to the subjects compared to the *non-social* hiding. At the same time after the hiding marmosets looked less at the hiding places ("A" + "B") in the *social* condition both in the "A" ($Z=3.827$; $p<0.001$) and in the "B" ($Z=3.010$; $p=0.003$) trials, as they spent a considerable amount of time looking at the human experimenter. These results suggest that the presence of a human experimenter attracts the attention of marmosets, but this distraction effect is not enough to influence subjects' performance in the "A-not-B" task.

Our results thus show that, in contrast to human infants (Topál et al. 2008), the marmosets' success in the "B" trials was not influenced by the communicative context of the hiding e.g. the Natural Pedagogy hypothesis cannot account for the "A-not-B" error committed by common marmosets. These results seem to be in line with arguments stating that though non-human animals may well be similarly sensitive to eye-contact as humans are, the meaning of this signal can still vary across species (Csibra 2010). Up to now there has been no evidence showing that animals, with the possible exception of the domestic dog, would interpret eye-contact as a signal that calls for attributing additional meaning to the others' behaviour. In the present experiment we directly examined this question and found negative results.

On the other hand, we found that the trajectory of the hiding in the "B" trials influenced the marmosets' success. In the asymmetric test (when the target object first crossed location "A" before arriving to location "B") the monkeys made more mistakes than in the symmetric test. This difference may be explained by the fact that in the "B" trials, hiding took longer in the asymmetric test than in the symmetric tests, posing increased attentional demands. The attention span of common marmosets is rather short and the individual variation is high (Range & Huber 2007), which can result in a difference in their success between the two tests. Alternatively or in parallel, the asymmetric test is likely to have higher memory requirements. Crossing location "A" in the "B" trials in the asymmetric test might have strengthened the memory of having the target in this location. Based on these results it seems that the marmosets' limited attentional and/or memory capacities contribute to their decreased success in the "B" trials compared to the "A" trials.

PART III: Species adapted to the human environment

Apart from the above outlined phylogenetical approach that is based on behavioural homologies, in recent years another approach, based on behavioural analogies, has also attracted a lot of attention (e.g. Hare et al. 2002). This approach studies the socio-cognitive skills of domestic species that have adapted to the human niche. Comparing the behaviour of these species to that of their wild living relatives reveals the effect of the human environment.

The domestic dog as a model of human behaviour⁴

The domestic dog (*Canis familiaris*) is the first and foremost common model species of the comparative approach based on behavioural analogies. During domestication the dog has acquired complex socio-cognitive skills, such as attachment to the human caregiver (Topál et al. 1998), or following of human referential pointing gestures (Riedel et al. 2008). Based on these and other behaviours domestic dogs differ markedly from their closest wild relative, the wolf (Miklósi et al. 2003; Gácsi et al. 2009), and they even outperform chimpanzees in several socio-cognitive tasks (Tomasello & Kaminski 2009; Kirchhofer et al. 2012).

Background

The above described “A-not-B” error was long thought to be non-existent in dogs (Gagnon & Doré 1992). Recently, however, it was found that adult pet dogs, similarly to human infants, also commit the A-not-B error in the presence of ostensive communicative cues of the experimenter (Topál et al. 2009b). However, the exact nature of dogs’ responsiveness to human communicative signals and its role in inducing the perseverative search error are still unknown (Tomasello & Kaminski 2009). Accordingly, an ongoing debate discusses whether the errors made by dogs are caused by similar processes as in infants or whether simpler learning processes or confounding effects of procedural factors can account for them (Fiset 2010; Marshall-Pescini et al. 2010). In this chapter we address in three studies questions related to these alternative hypotheses.

Study I.

Fiset (2010) argues that, 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”. 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 (see e.g. Hartshorne 2008). In infants it has been shown that they reliably reach back to location “A” even though they saw that the object went straight to the “B” hiding place without getting in contact with “A”

⁴ This chapter is based on: **Sümegei, Z., Kis, A., Miklósi, Á., & Topál, J. (2014).** Why do adult dogs (*Canis familiaris*) commit the A-not-B search error? *Journal of Comparative Psychology*, **128**, 21–30.; **Kis, A., Topál, J., Gácsi, M., Range, F., Huber, L., Miklósi, Á., & Virányi, Z. (2012).** Does the A-not-B error in adult pet dogs indicate sensitivity to human communication? *Animal Cognition*, **15**, 737–743.; **Topál, J., Miklósi, Á., Sümegei, Z., & Kis, A. (2010).** Response to comments on “Differential sensitivity to human communication in dogs, wolves, and human infants” *Science*, **329**, 142–d.

Procedure

Before the test trials, subjects participated in two warm up trials. In these trials only one screen was placed on the floor and the experimenter placed the toy behind it in full view of the dog that was then released to search for it. Only those animals were included in the next phase that did not show any sign of distress and were motivated to fetch the toy.

Test trials consisted of four “A” and three subsequent “B” trials. Depending on the group they were assigned for, subjects witnessed one of three different hiding procedures. The video protocol can be found at: <http://www.cmdbase.org/web/guest/play/-/videoplayer/116>

In the ‘*Communicative Hiding*’ group (*Com-H*, N = 20) we aimed to reproduce earlier findings and therefore we applied the same procedure reported in Topál et al.’s study (2009). During the “A” trials the experimenter addressed the subject (dogs’ name + “Look!” in a high pitch voice), she approached the toy, picked it up and captured the dog’s attention with the toy in hand (by establishing eye-contact and addressing the dog). Then she walked to the adjacent screen (“A”) and placed the toy behind it. Finally, after walking behind screen “B”, the experimenter returned to the dog that was released by the owner. If the subject chose the baited screen, it was praised and allowed to play with the toy for a few seconds. If the subject visited the empty screen first, it did not get the toy but was called back and praised verbally by the owner. The whole procedure was repeated three more times.

Immediately after the four “A” trials, three “B” trials followed. These were similar to the “A” trials, except that the experimenter did not leave the toy behind screen “A”, but instead the toy visibly re-emerged in her hand and she showed the toy to the dog while looking at it. Then she placed the toy behind screen “B” and returned to the dog that was allowed to make a choice.

Testing a second group of dogs, the so called ‘*Alleviated B trials*’ group (*Allev-B*, N = 34) we aimed to control for the ‘sham baiting’ that occurred in the “B” trials of the *Com-H* procedure. In this condition, dogs witnessed the same hiding procedure as dogs in *Com-H*, 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 *Com-H*, while holding the toy visibly in her hand at the height of her eyes and looking continuously at the dog.

In the ‘*Only watching during A trials*’ group (*Watch-A*, N = 26) 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 *Com-H* with the only exception 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. Having retrieved the toy 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 *Com-H*.

All tests were videotaped for later analysis.

Data analysis

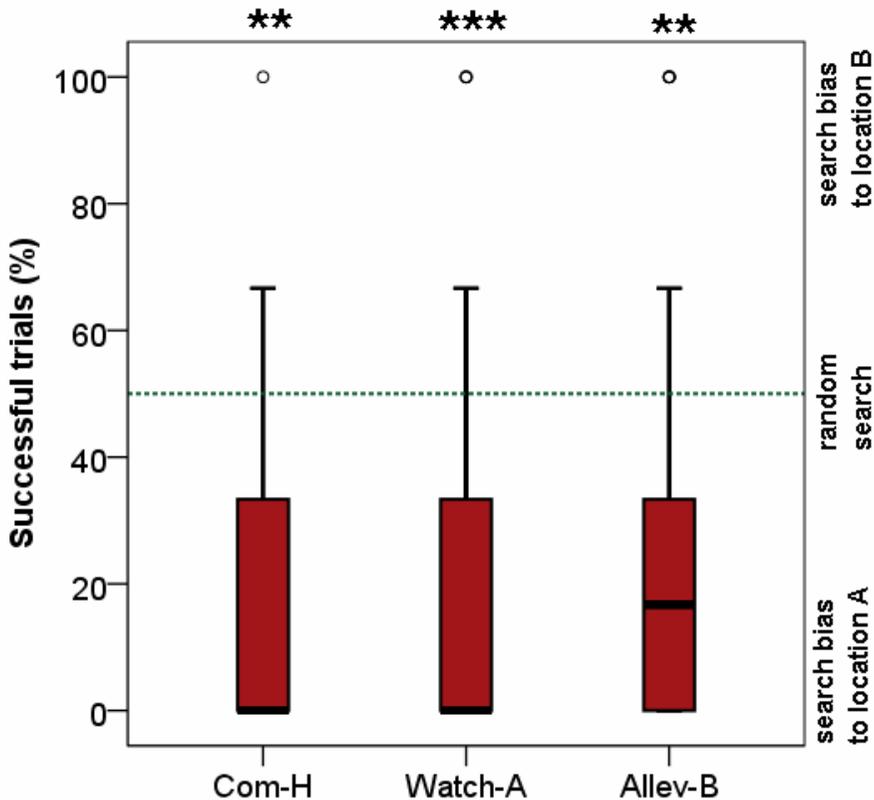
In all groups, the first inspected location was regarded as the subject’s choice. A choice was scored if the dog touched the screen with its nose or paw. Dogs received scores of 1 or 0 depending on whether they chose the baited or the empty location respectively. In very few

cases (5 trials out of 456) the dogs made an ambiguous choice (they passed along the midline between the screens having equal visual access to the content of both hiding places and made their choice only afterwards); these trials were excluded from the analysis.

The percent of correct choices in the three “B” trials (one sample Wilcoxon Signed-rank test) as well as the choice in the first “B” trial (Binomial test) was compared to the 50% chance level in the case of all groups. Furthermore, pair-wise comparisons between the *Com-H* and the modified conditions were performed (Mann-Whitney test).

Results and Discussion

Dogs fetched the object reliably from behind screen “A” during the “A” trials, choosing the empty screen only 2 times out of 216 trials. 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 (one sample Wilcoxon Signed-rank tests) not only in the ‘*Com-H*’ (T=-174, p=0.008) but also in the ‘*Allev-B*’ (T=-488, p<0.001) and ‘*Watch-A*’ (T=-288, p=0.003) groups (Figure 8). Choice behaviour in the first “B” trials (Binomial test, test proportion: 0.5) showed a similar below chance performance in the ‘*Com-H*’ (p=0.008), ‘*Allev-B*’ (p=0.001) and ‘*Watch-A*’ (p=0.001) conditions.



8. figure Percent of correct responses (median, quartiles and extremes) in the 3 “B” trials as a function of the hiding procedure in comparison with success rate expected by random choice (50%). One sample Wilcoxon signed rank test; **: $p < 0.01$, ***: $p < 0.001$

In the ‘*Com-H*’ group, screen “A” was sham-baited just like in Topál *et al.* (2009). In ‘*Watch-A*’ group the dog was just a bystander during the “A” trials. In ‘*Allev-B*’ group, screen “A” was not revisited by the experimenter during the “B” trials.

Pair-wise comparisons (Mann-Whitney tests) of the subjects' performance in the "B" trials between '*Com-H*' and the modified conditions failed to show any effect of 'sham baiting' in the "B" trials ('*Com-H*' versus '*Allev-B*'; $U=336$, $p=0.937$) as well as of actively searching in the "A" trials ('*Com-H*' versus '*Watch-A*'; $U=250$, $p=0.803$).

In sum, we found that dogs tended to commit the "A-not-B" error even though the situation was attentionally less demanding when no 'sham baiting' occurred in the "B" trials. Furthermore, subjects 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 dogs' inability to inhibit previously rewarded motor response or their insufficient working memory and/or attention skills cannot explain their erroneous choices in this "A-not-B" error task.

Study II.

In Study I. we found indirect support for the claim that dogs commit the "A-not-B" error due to the human experimenter's ostensive cues by excluding two alternative hypotheses that have been previously proposed. In Study II. we aimed at directly investigating the effect of ostensive-communicative cues on dogs' search behaviour in the same "A-not-B" error task. The original study by Topál et al. (2009a) tested the crucial role of dogs' susceptibility to human communicative signals in an "A-not-B" search error task by consistently manipulating the communicative aspect of the hiding procedure in both the "A" and "B" trials. In one condition, they hid the reward in a non-social manner (the ball was moved around using an invisible string attached to it) and in this case most dogs succeeded to find the hidden object without making the "A-not-B" error. They also tested dogs in social conditions, in which a human experimenter carried the ball around after calling the dogs' attention both in the "A" and "B" trials either in an ostensive (addressing the dogs by saying "Dogs' name + Watch!" and making eye-contact with it) or in a non-ostensive (squeezing the toy) manner. Perhaps the most interesting finding of this study was that, albeit in both social conditions the toy was hidden by a human experimenter, dogs committed the "A-not-B" error only more frequently in the ostensive condition as compared to the non-ostensive one. These findings suggested that dogs' response to human communication is primarily driven by a motivation to satisfy ostensively cued human imperatives even when leading to an inefficient or mistaken solution. However, as it was pointed out by Tomasello and Kaminski (2009), in the original '*Com-H*' condition, the experimenter addressed the dog ("Name+Watch!" and eye-contact) at the "A" hiding place, but gave only limited ostensive cues (eye-contact) to the dog before hiding the object in location B. Although communicative, dogs did not follow these limited ostensive cues directed to location "B", suggesting that dogs acquire generic information during the "A" trials and tend to rely on this knowledge when making their choice in the "B" trials. Alternatively, one can argue that dogs' erroneous choices in the "B" trials are caused by the current signals provided by the experimenter.

In adherence to the later argument, assuming that eye-contact has less influence on dogs compared to a combination of different ostensive cues ("Dogs' name + Watch!", high-pitch voice and eye-contact), it can be assumed that dogs will prefer the better enhanced "A" location over location "B" as shown in the original '*Com-H*' condition. This later hypothesis has been confirmed by Marshall-Pescini and colleagues (2010) who found that, after being addressed

ostensively (“Dogs’ name + Watch!” and eye-contact) both at the “A” and “B” locations, dogs were no more biased toward location “A” making fewer erroneous choices. This procedure, however, differed from the ‘Com-H’ condition (both in the original study by Topál et al., 2009 and in the present study) not only in the distribution of ostensive cues in the “B” trials but also in that the experimenter did not return to the initial position after the hiding procedure, instead staying at the “B” side possibly attracting the dogs to location “B” (Marshall-Pescini, personal communication).

Therefore, in order to investigate to what extent the presence of ostensive cues in the “B” trials close to location “A” and “B” influences the “A-not-B” error of dogs, we tested two groups of dogs with two extreme versions of the “B” trials when either only location “A” or only location “B” was highlighted by the experimenter’s ostensive cues. In the former group, dogs may be driven to choose location “A” also in the “B” trials by the experimenter’s imperatives received in the “A” trials as well as during the recent hiding procedure of the “B” trials. Whereas in the later group the experimenter’s earlier and recent ostensive cues suggest conflicting choices. Consequently, if the choice of dogs in the “B” trials is adjusted to the experimenter’s cues given during the preceded hiding, we expect them to choose location “B” in this group. If, however, dogs commit the “A-not-B” error because they tend to follow the imperatives the experimenter communicated to them in the “A” trials also in the “B” trials, they should choose location “A” in the later group. In order to eliminate all other factors that may remind dogs of the former “A” trials, location “A” was not ‘sham-baited’ in the “B” trials. That is the hiding procedure was the same as on the ‘*Allev-B*’ group in Study I.

Methods

Subjects

Adult pet dogs (N=37) from 14 different breeds participated in the study (23 males, 14 females; mean age: 4.4 ± 3.4 years). They were assigned to two different groups quasi-randomly so that the distribution of age and gender did not differ across groups. None of the subjects had to be excluded from the study.

Experimental arrangement

The experiments took place in a room (3.9 m x 4.1 m) at the Eötvös University, Budapest where two opaque plastic boxes (30 cm wide x 50 cm high x 30 cm deep) were placed 0.6 m apart to hide the toy. The owner held the collar of the dog that was facing the screens standing equidistant (2 m) from them. A rubber toy was placed on the floor 0.6 m from the left or the right screen (counterbalanced across dogs) in line of the screens.

Procedure

Before the test trials, subjects participated in two warm up trials where only one screen was placed on the floor using the same procedure as in Study I. Test trials consisted again of four “A” and three subsequent “B” trials. Depending on the group they were assigned to, subjects witnessed one of two different hiding procedures. The dogs in both groups watched the same hiding as in the ‘*Allev-B*’ condition of Study I. with modified “B” trials involving ostensive communicative cues (addressing and eye contact) only at location “B” (‘*Communicative cues only at B*’ group - 0^A-Com^B , N = 18) or only at “A” (‘*Communicative cues only at A*’ group - $\text{Com}^A\text{-}0^B$, N = 19).

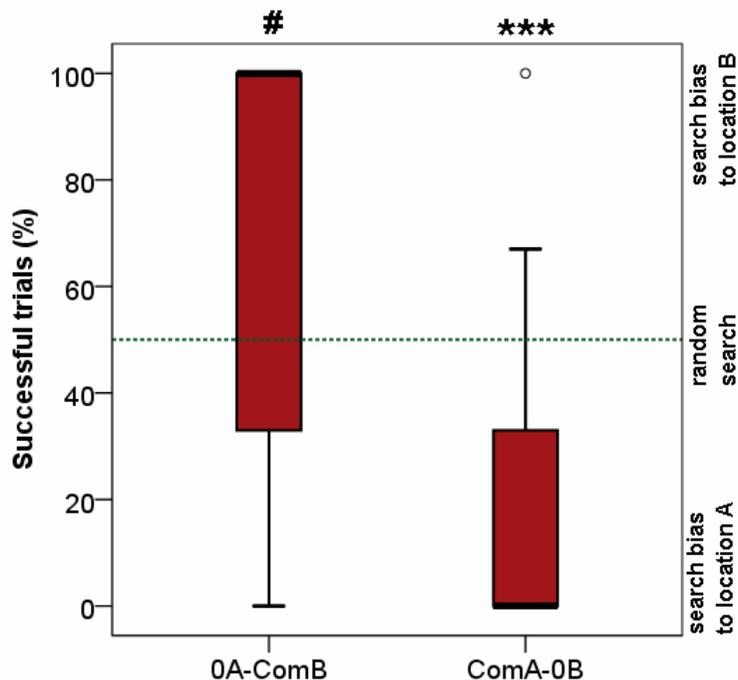
Elimination of the ‘sham-baiting’ to the “A” hiding place during the “B” trials (*Allev-B*) did not have an effect on the dogs’ performance (compared to the original *Com-H* condition) – see above. However, in order to prevent any possible interactions between the higher demands on working memory (caused by the ‘sham baiting’) and other factors to be tested, we decided to modify the ‘*Allev-B*’ condition instead of the ‘*Com-H*’ condition.

Data analysis

Data analyses were carried out in exactly the same way as in Study I. with comparisons to the 50% chance level (Wilcoxon signed rank test, Binomial test) and pair-wise comparisons to the original *Allev-B* group (Mann-Whitney test). Only one out of the 259 trials was excluded due to ambiguous choice.

Results and discussion

Dogs fetched the object reliably from behind screen “A” during the “A” trials, choosing the empty screen only once in 148 trials. During the “B” trials, subjects displayed perseverative search bias to the empty (“A”) location performing well below the success rate expected by random search (one sample Wilcoxon Signed-rank tests) in the ‘ Com^A-0^B ’ ($T=173.5$, $p<0.001$) group. In contrast, dogs in the ‘ 0^A-Com^B ’ group showed a trend towards an above-chance performance ($T=-45$, $p=0.081$) (Figure 9). Choice behaviour in the first “B” trials (Binomial test, test proportion: 0.5) showed a similar below chance performance in the ‘ Com^A-0^B ’ ($p=0.019$) condition and chance performance in the ‘ 0^A-Com^B ’ ($p=0.481$) condition.



9. figure Percent of correct responses (median, quartiles and extremes) in the 3 “B” trials as a function of the hiding procedure in comparison with success rate expected by random choice (50%). One sample Wilcoxon signed rank test; #: $p<0.1$, ***: $p<0.001$.

Ostensive communicative cues (eye contact and addressing) in the “B” trials were given only at location “B” in 0^A-Com^B group and only at location “A” in Com^A-0^B group.

Pair-wise comparisons (Mann-Whitney tests) of subjects’ performance in the “B” trials did not show a significant effect of capturing the dogs’ visual attention (eye-contact) before hiding

the object at the “B” location in the ‘*Allev-B*’ compared to the ‘*Com^A-0^B*’ condition (U=169.5, p=0.569). However, adding salient ostensive signals (addressing the dog in high pitch voice while making eye-contact) at location “B” and avoiding such signals at location “A” during the “B” trials (‘*0^A-Com^B*’) successfully reduced the perseverative search bias. Dogs in the ‘*0^A-Com^B*’ condition committed significantly less search errors compared to ‘*Allev-B*’ (U=79, p=0.003).

In sum, we can say that removing eye-contact at location “B” in the “B” trials did not increase dogs’ tendency to perseverate. On the other hand, in the modified “B” trials that involved addressing the dogs ostensively at “B” while giving no such cues at “A” decreased their error rate.

Study III.

Study II. has found that ostensive cues given during the “B” trials substantially influence dogs’ performance in an “A-not-B” search task. Similarly, another study by Sümeği et al. (2014) systematically manipulating communicative and non-communicative cueing during the “A-not-B” task also found that communicative signals presented at the “A” hiding place during the “B” trials but not during the “A” trials play a crucial role in inducing the “A-not-B” error. Based on these results in Study III. we expected to induce “A-not-B” error in dogs without performing any “A” trials. Although Study I. has showed that local enhancement or ‘sham-baiting’ of the “A” hiding place does not alter dogs’ perseverative response in the “A-not-B” context, here we hypothesized that in the ‘only B trials’ condition it becomes crucial whether or not the “A” hiding place is enhanced by the experimenter’s ostensive communicative cues. Thus we planned a hiding procedure in which in addition to omitting the “A” trials we used three different types of “B” trials: a *Social-Communicative* condition (see Study I.) in which during the “B” trials the dog’s attention is directed to location “A” (‘sham-baiting’) after ostensively addressing the dog; the so called *Alleviated B trials* condition (see Study I.) in which this ‘sham-baiting’ is omitted and the experimenter goes directly to location “B”; and a *NonCommunicative* control condition (see Topál et al. 2009a).

Methods

Subjects

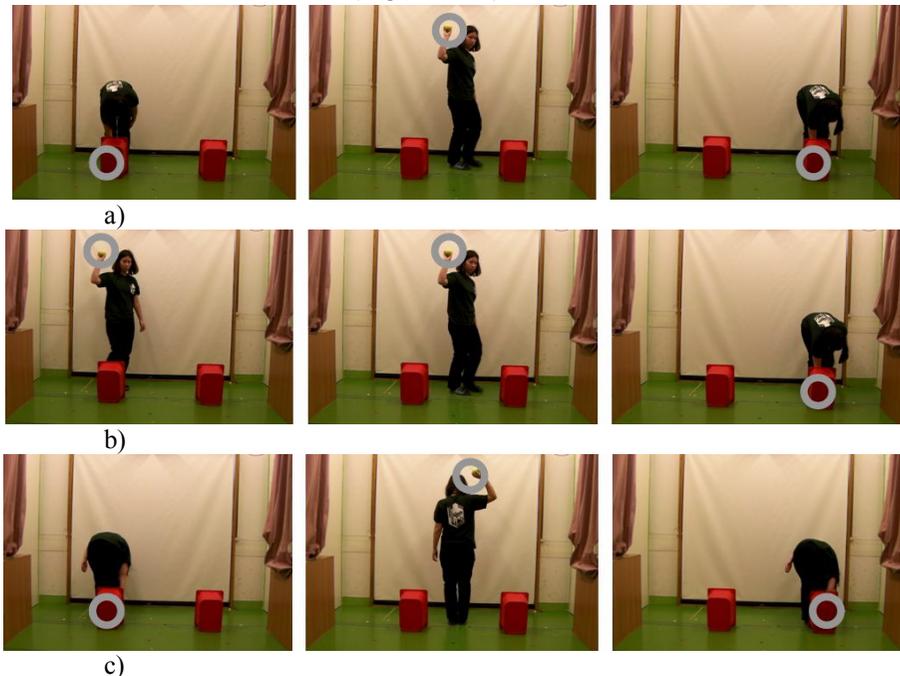
Sixty five task-naïve adult (>1 year) pet dogs participated in the study (29 males, 34 females; mean age: 3.92 ± 2.52 years). They were from 17 different breeds and 22 mongrels. Two dogs had to be excluded due to under-motivation. Subjects were assigned to three hiding contexts (see below) so that the distribution of age would not differ across conditions.

Procedure

The experiment was conducted in a room (3.9 m x 4.1 m) at the Eötvös University with the same experimental arrangement as in Study I. (Figure 7). Before the test trials, subjects participated in two warm up trials with only 1 screen placed on the floor (halfway between subsequent locations “A” and “B”) and the experimenter hid the ball behind it in full view of the dog that was then released to search for it. If the dog was unwilling to search it was encouraged by the owner.

Test trials consisted of three “B” trials without any previous “A” trials. Depending on the experimental group subjects witnessed one of three different hiding procedures.

In the ‘*Communicative Hiding*’ group (*Com-H*, N = 21, 14 males, 7 females) we aimed to test the role “A” trials play in inducing the “A-not-B” error, thus the hiding procedure was the same as reported in previous studies (see e.g. Study I.) with the only difference that the “A” trials were omitted. During the three “B” trials the experimenter addressed the subject (dog’s name + “Look!” in a high pitched voice), she approached the toy, picked it up and captured the dog’s attention with the toy in her hand (by establishing eye-contact and addressing the dog). Afterwards she walked to the adjacent screen (“A”) and placed the toy behind it, than the toy visibly re-emerged in her hand and she showed the toy to the dog while looking at it. Finally she placed the toy behind screen “B”, returned to the dog showing her empty hands and the subject was allowed to make a choice. (Figure 10/a)



10. figure Hiding procedure for the a) ‘*Com-H*’, b) ‘*Allev-B*’ and c) ‘*NonCom*’ conditions.

Testing a second group of dogs, the so called ‘*Alleviated B trials*’ group (*Allev-B*, N = 21, 8 males, 13 females) we aimed to test the role ‘sham baiting’ of the “A” hiding place plays in inducing the “A-not-B” error. Thus in this condition, dogs witnessed the same hiding procedure as previously described in *Com-H* (subjects were addressed in a communicative way, by calling their name and making eye-contact), with the only exception that the experimenter did not ‘sham bait’ the toy behind screen “A”. She walked up to screen “B” following the same track as in the *Com-H*, while holding the toy visibly in her hand at the height of her eyes and looking continuously at the dog. (Figure 10/b)

Finally as a control group we tested a group of dogs in the ‘*Non-Communicative Hiding*’ condition (*NonCom*, N = 21, 7 males, 14 females) following the procedure described in Topál et al. (2009) with the only difference that the “A” trials were omitted. The experimenter attracted the dog’s attention by clapping her hands then she approached the toy and made a beeping sound with it without facing the dog. Afterwards she walked to the adjacent screen (“A”) with her back turned towards the dogs and placed the toy behind it, than the toy visibly re-emerged and made a beeping sound while the experimenter was still turned with her back.

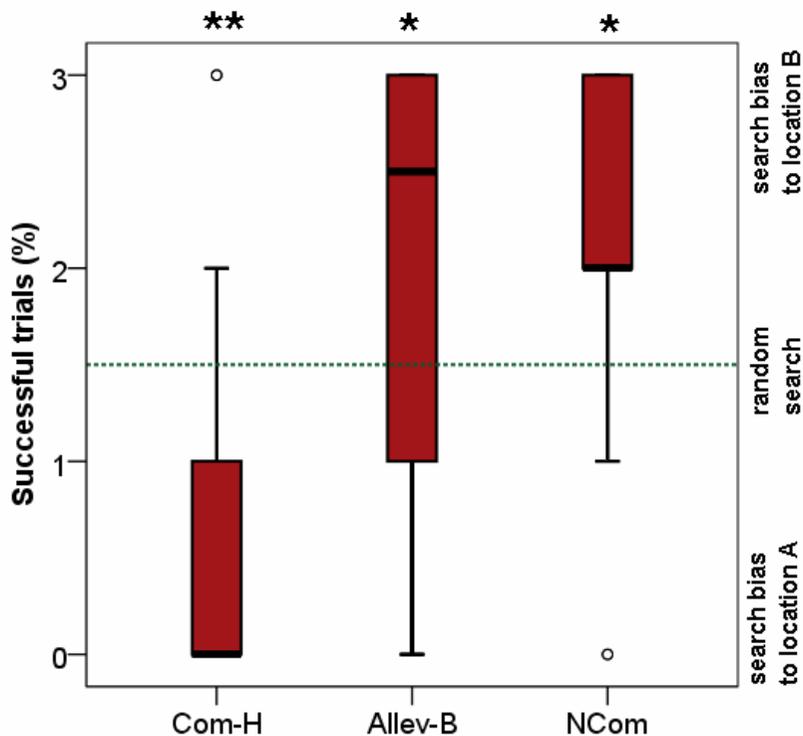
Finally she placed the toy behind screen “B”, returned to the dog showing her empty hands and the subject was allowed to make a choice. (Figure 10/c)

Data analysis

The number of correct choices in all three groups was compared to the 50% chance level using a one-sample Wilcoxon signed rank test. Furthermore, planned pair-wise comparisons between ‘Com-H’ and ‘Allev-B’ as well as ‘Com-H’ and ‘NonCom’ conditions were performed (Mann-Whitney tests).

Results and discussion

In the ‘Com-H’ condition subjects displayed a search bias to the empty (“A”) location performing well below the success rate expected by random search (25% correct, $T=-190$, $p=0.008$) in the three “B” trials despite the fact that location “A” had never been baited. On the contrary when ‘sham baiting’ at “A” was omitted (‘Allev-B’ condition) subjects performed above chance (70% correct, $T=49$, $p=0.019$), thus achieving a significantly higher number of correct choices than subjects in ‘Com-H’ ($U=84$, $p<0.001$). Moreover in the ‘NonCom’ group (with ‘sham baiting’ but no communicative cuing at location “A”) dogs also performed above chance (68% correct, $T=51$, $p=0.023$) and achieved a higher number of correct choices than subjects in the ‘Com-H’ condition ($U=87$; $p<0.001$) (Figure 11).



11. figure Number of correct choices in the different hiding conditions; median, quartiles, whiskers, outliers. Comparisons to the 50% chance level (Wilcoxon signed rank test) (* $p < 0.05$; ** $p < 0.01$).

The analysis based only on the first test trials in the different conditions shows quite similar results. Dogs in the Com-H group preferred to choose the empty “A” location (binomial test, test proportion: 0.5; $p = 0.027$; only 5 dogs of the 21 ones chose the baited location) while dogs in the ‘Allev-B’ and ‘NonCom’ groups showed a non-significant trend towards above chance

performance (binomial test, test proportion: 0.5; $p = 0.078$; 15 dogs from the 21 ones selected the baited location in both conditions).

These results are in line with findings in Study I. & II. and further confirm the hypothesis that “A” trial is not an indispensable part of the procedure inducing “A-not-B” error in adult dogs. In addition, it seems that ‘sham-baiting’ at location “A” and the attraction of the dogs’ attention by ostensive addressing signals next to the “A” location can both play a role in eliciting erroneous choices. A summary of the present results and findings from recent studies (Table 1) indicates that communicative (vs. non-communicative) cuing and other attention-directing acts (‘sham baiting’) affect dogs’ search bias in an interactive manner.

	Cuing next to “A” during “A” trials	Cuing next to “A” during “B” trials	Sham baiting at “A” during “B” trials	Search bias	Source
Com-H	–	Comm	Yes	Towards the empty (“A”)	Study III.
	Comm	Comm	Yes	Towards the empty (“A”)	Study I.
NonCom	–	NonComm	Yes	Towards the baited (“B”)	Study III.
	NonComm	NonComm	Yes	No search bias	<i>Topál et al. 2009</i>
Allev-B	–	Comm	No	Towards the baited (“B”)	Study III.
	Comm	Comm	No	Towards the empty (“A”)	Study I.

1. table Summary of results and comparison of findings from Study I & III. Comm: eye contact & verbal addressing (dogs’s name + Watch!); NonComm: squeaking the toy while back-turned; –: no attention getting signal.

This table clearly shows that sham baiting of the “A” screen without directing the dog’s attention towards that location in an ostensive-communicative manner is insufficient to elicit the “A-not-B” error in dogs. Moreover both the presence/absence and the timing of ostensive addressing signals are of great importance: Cues including eye contact and verbal addressing compared to non-communicative salient attention-getters (squeaking the toy) are more effective in inducing the dog to select the empty (“A”) location especially if the experimenter provides these signals next to the “A” location during “B” trials. Importantly, however, the communicative cuing next to the “A” location during “B” trials can increase the dogs’ tendency to commit “A-not-B” error if, and only if it is either complemented with sham baiting of the “A” screen or the “A” location was previously repeatedly baited in an ostensive communicative context.

In sum the present findings are in line with the view that, like in infants (Longo & Bertenthal 2006; Topál et al. 2008), 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. It is still debated, however, whether dogs follow the enhancing effect of the

most recently viewed human cues (as delivered on the “B” trials) or they recall generalizable information extracted from earlier human behaviour (during the “A” trials) that dogs may interpret as imperative orders. Therefore, we further investigated the question whether human ostensive cues given either at location “A” or at location “B” during the “B” trials have an influence on the choice behaviour of the dogs if the preceding “A” hidings remain the same. We tested dogs in a condition where in the “B” trials all communicative cues were eliminated at the “B” hiding place (that is the experimenter did not make eye-contact with the subjects as in the original study), and we found that this modification did not influence the dogs’ performance. This can be explained by the dogs being sensitive only to some human-given ostensive cues (e.g. high pitched voice but not eye contact) in situations like the “A-not-B” task. However, a more parsimonious explanation for our results would be that due to a floor effect in the ‘*Com-H*’ and ‘*Allev-B*’ conditions subjects could not make significantly more errors even when we removed the eye contact at location “B”.

More importantly, when in the “B” trials the experimenter ostensibly cued location “B” in contrast to her former imperatives in the “A” trials to visit location “A”, dogs showed reduced search bias towards location “A” compared to the ‘*Allev-B*’ condition. This indicates that the local enhancing effect of recent ostensive cues delivered in the “B” trials has a crucial role in directing the search response of the dogs. Nevertheless, dogs did not show a clear preference to location “B” in spite of the recent cuing of the experimenter as well as of the reward being hidden here. The conflicting information of the preceding “A” trials also seems to have a strong influence on the choices of the dogs (see also Topál et al. 2010 for similar results). Since in our ‘*0^A-Com^B*’ group, despite of watching location “B” exclusively cued, the dogs chose location “B” less often than they did in the study by Marshall-Pescini et al. (2010) who provided ostensive cues at both locations, it seems likely that in their study the experimenter’s final position close to location “B” made dogs show a clear preference for location “B”. Accordingly, we conclude that human-given ostensive cues can influence the choice behaviour of dogs by the immediate effect of enhancing certain locations or objects as well as by transmitting generalizable information that is valid at least as long as the human signaller is present (Topál et al. 2009b; Kupán et al. 2011).

Our results also support the notion that the communicative and non-communicative signs have different effects in this task (see also Topál et al. 2009; Sümegei et al. 2014). Thus we cannot exclude the possibility that dogs’ erroneous choices in the “B” trials stems from their disposition to act in line with a human demonstration. This account suggests that the experimenter’s ostensive addressing signals during object-hiding events acted as not only making the subject recognize the location of the toy but manifesting a specific behaviour.

In agreement with recent studies we also found that dogs in object search tasks (Bräuer et al. 2006; Erdőhegyi et al. 2007; Kupán et al. 2011) rely on human communicative gestures. An interesting aspect of our findings is that the selection of the empty (“A”) location can be elicited without any previous “A” trials and the ostensive addressing signals presented next to the “A” location during “B” trials plays a key role in committing search errors. This seemingly contradicts with the results of (Osthaus et al. 2010) showing that the number of “A” trials plays a crucial role in inducing the “A-not-B” error. But this can be explained by the fact that they

used a different method (dogs had to make a detour through a gap at one end of a straight barrier in order to reach a target) with a non-communicative hiding procedure.

In summary, the present study provides evidence that contrary to previous assumptions in the case of adult pet dogs no “A” trial is needed to induce the “A-not-B” error. The finding that search performance is affected by the ostensive communicative signals presented at location “A” during the “B” trials suggest that the phenomenon, at least partially, reflects a ‘ready-to-obey’ attitude in the dog rather than insufficient attention and/or working memory. Results from previous research have already suggested that domestic dogs readily adopt inefficient responses in object choice tasks as a result of repeated observations of human action demonstrations (Kupán et al. 2011), and their sensitivity to human social cues may lead to apparently faulty behaviours (Erdőhegyi et al. 2007; Kaminski 2009). Such a disposition, that 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.

Another domestic species: ferrets⁵

Background

We have seen in the previous chapter that dogs have become famous for their sophisticated socio-cognitive abilities (e.g. Hare et al. 2002; Miklósi et al. 2003). Many think that these abilities have been formed by the cognitively challenging complex human social environment (Hare et al. 2002; Gácsi et al. 2009) and, as a consequence of the shared environment, some rudimentary social-cognitive skills such as interspecific attraction and/or sensitivity to human social cues may have developed in some of the domestic species; but see Udell et al. (2011). Through this evolutionary process, the dog as a species has moved from the niche of its ancestor to the human social environment (Miklósi et al. 2004). In this new niche dogs have formed a close social relationship with their human partners due to their dependent social position (e.g. “attachment” Topál et al. 1998), and a flexible system for interspecific communication has also emerged (Pongrácz et al. 2005). Alternatively or in parallel to these hypotheses, one might expect the socio-cognitive abilities of dogs resulting from their extensive hand rearing and individual socialization to the human environment from a very early age on. One way to find out the role of domestication in the emergence of these special abilities is to study other domesticated species and their wild counterparts as well.

Although surprisingly little is known about the socio-cognitive abilities of domesticated species other than dogs, the effects of domestication are probably not limited to canids and therefore the comparative exploration of the phenomenon is important. Although the methods used in different experiments vary considerably, recent studies found that domestic cats (Miklósi et al. 2005), horses (Maros et al. 2008), goats (Kaminski et al. 2005) and pigs (Nawroth et al. 2014) are also able to follow certain types of human pointing gestures in order to locate hidden food. Furthermore, experimentally domesticated fox kits (selected for tameness for over 45 years) were also found to be more skilled to follow human pointing gestures than fox kits from a control population (Hare et al. 2005). Although data on the wild

⁵ This chapter is based on: **Hernádi, A., Kis, A., Turcsán, B., & Topál, J. (2012).** Man’s underground best friend: domestic ferrets, unlike the wild forms, show evidence of dog-like social-cognitive skills. *PLoS ONE*, 7, e43267.

counterparts of the above species is still lacking these findings are in line with the notion that, similarly to what has been found in dogs (Gácsi et al. 2009), domestication as a special evolutionary process might have led to changes in attention and willingness to cooperate with humans that can cause performance differences in certain socio-cognitive tasks.

Ferrets – a carnivore species of the Mustelidae family originating from wooded and semi-wooded areas (Lodé 1999) – have not yet been experimentally studied in socio-cognitive tasks relating to humans. Although their early history in service of man is obscure, ferrets have probably been domesticated for more than two thousand years (Thomson 1951) by selective breeding from the European polecat (*Mustela putorius*) (Lodé 2008). Similarly to dogs, ferrets have been bred originally for practical functions (hunting) (Price 2002), but nowadays many of them are merely kept as pets (for more details about the history and domestication of *Mustela* see Vinke & Schoemaker, 2012). This, and the fact that ferrets are increasingly popular as companion animals and thus the study of their behaviour and welfare has begun recently (Talbot et al. 2014), makes them an ideal subject to study the effect of domestication on their human related socio-cognitive skills as it seems likely that similarly to dogs (and potentially other domesticated pets), ferrets also adapted to the human niche. Therefore we assumed that in contrast to wild *Mustela*, domestic ferrets will show similar behavioural patterns as dogs in socio-cognitive tests. We predicted that both domestic species would show (i) increased tolerance of eye-contact with their owner vs. a stranger, (ii) preference towards their owner as opposed to a stranger when having to decide from whom to get a piece of food and (iii) utilization of human pointing gestures in order to locate hidden food.

Methods

Subjects

Three groups of subjects were tested. The first group consisted of 17 privately owned domestic ferrets (*Mustela furo*) (mean age \pm SD: 3.6 \pm 1.7, 11 males). The second group consisted of 16 privately owned wild *Mustela* \times domestic ferret hybrids (wild blood ratio ranged from 1/1 – 1/16, meaning 0-4 crossbreedings between wild and domestic lines; mean age \pm SD: 2.8 \pm 2.3, 7 males; 8 European polecat (*Mustela putorius*) hybrids, 4 Steppe polecat (*Mustela eversmanii*) hybrids, 3 European mink (*Mustela lutreola*) hybrids, 1 Siberian weasel (*Mustela sibirica*) hybrid). The third group consisted of 18 adult domestic dogs (*Canis familiaris*) (mean age \pm SD: 3.5 \pm 2.7, 7 males). Dogs were chosen from small sized breeds (less than 10 kg of weight which were originally bred to hunt and kill vermin (similarly to ferrets) according to their breed standard descriptions (www.fci.be, www.akc.org) (4 Dachshunds, 3 Jack Russell terriers, 3 Chinese naked dogs, 3 Dwarf schnauzers, 3 Yorkshire terriers, 2 West highland white terriers). Domestic ferrets were all kept in an outdoor enclosure. They entered the house of the owner only occasionally but had daily human contact. Members of the wild *Mustela* hybrid group were either kept in an identical way (N=6) or lived permanently in the owner's flat thus having prolonged human contact (N=10) compared to the domestic ferrets. Keeping conditions for domestic dogs varied from living in a garden without entering the owner's house to living permanently inside the house, but they all had daily human contact.

Procedure

Tests were carried out by three female experimenters with two of them being present at the same time) in a room unfamiliar to the subjects. Domestic ferrets and wild *Mustela* hybrids

were tested at their owners' home in a room that was not familiar to them, while domestic dogs were tested in a room at the Eötvös University. Testing was preceded by a 5-minutes-long habituation period when subjects were allowed to explore the room freely.

Subjects of all groups were engaged in three tests measuring their human-related social behaviours. Some of the subjects had to be excluded due to technical problems (e.g. owner not following the instructions) or because the subject was not willing to participate (see sample sizes for each test). All tests were videotaped for later analysis.

Tolerance of eye-contact

Following the habituation period a female experimenter (E1) and the owner (in a counterbalanced order across subjects) made eye-contact with the subjects and was trying to maintain it for 30 seconds. At the beginning of the trial the human lifted the subject so that it was positioned at his/her face level. Both the owner and the experimenter were holding the subjects at the height of their face without restricting head-movements and tried to catch the subjects' attention by emitting sounds and/or gently moving the subjects. Post-test coding of the videos showed that both the owner and the experimenter spent the same amount of time talking to (domestic ferrets: $t_{(17)}=1.764$, $p=0.096$; wild *Mustela* hybrids: $t_{(15)}=1.678$, $p=0.114$; domestic dogs: $t_{(18)}=0.211$, $p=0.836$) and moving (domestic ferrets: $t_{(17)}=0.826$, $p=0.421$; wild *Mustela* hybrids: $t_{(15)}=1.742$, $p=0.102$; domestic dogs: $t_{(18)}=0.031$, $p=0.976$) the subjects.

We measured the total duration of the subjects looking at the face of the owner and the experimenter respectively with frame-by-frame analysis of the videos. Double coding of 30 videos showed an almost perfect inter-rater agreement (Cohen's kappa: 0.93). The performance in each group was analyzed by comparing the looking time at the owner versus at the experimenter with paired samples t-tests. The performance of domestic ferrets (the difference between the time looking at the owner and the time looking at the experimenter) was compared to that of wild *Mustela* hybrids and domestic dogs with independent samples t-tests. All statistical tests were two-tailed.

Sixteen domestic ferrets, sixteen wild *Mustela* hybrids and eighteen dogs completed the Tolerance of eye-contact test. 1 ferret was excluded due to technical problems (the owner did not follow the instructions).

Social-preference test

After the *Eye-contact* test subjects were engaged in a two way social choice test where they had to choose between a female experimenter (E2) and their owner. Both the experimenter and the owner were crouching 1 m apart from each other, holding a piece of food in their hand. E1 was holding the subject in the middle, 1 m apart from them forming a triangle. First both E2 and the owner simultaneously extended their hand towards the subjects and let them sniff their hands with the food in it while continuously talking. Then E1 released the subject and it could choose between the owner and E2 who were calling it. A choice was coded when the subject approached the hand of the human (owner/experimenter) to a distance of 2 cm or less, with score 1 for choosing the owner and score 0 for choosing the experimenter. The subject received the food from the chosen human but not from the other independently of its choice. If the subject did not approach any of the two humans within a 20 sec period, it was returned to the starting position and received a 0.5 score for that trial. If the subject refused to choose three times in a row, the test was terminated. This choice test was performed six times in total. E2

and the owner changed position (left/right) after each trial and their initial position was counterbalanced among subjects. Subjects that did not make any choice during the test were regarded as “not willing to participate” and were excluded from the analysis of this test (but were included in the other tests). The owner preference score was compared to the 50% chance level (Wilcoxon signed rank test) to analyze the performance in each group. The performance of domestic ferrets was compared to that of wild *Mustela* hybrids and domestic dogs with Mann-Whitney tests. All statistical tests were two-tailed.

Seventeen domestic ferrets, thirteen wild *Mustela* hybrids and eighteen dogs completed the test (with one wild *Mustela* hybrid completing only part of the trials). Three wild *Mustela* hybrids were not willing to participate.

Responsiveness to human gestures test

Sustained touching (6 trials). Following the social preference test subjects participated in the *Sustained touching* trials (without any pretraining with hiding food in the cups used for this test). E2 placed two cups (both baited with a piece of food) on the floor 1.5 m away from each other and crouched down in between. The owner was holding the subject in the middle 1 m away from E2. The experimenter called the subject’s attention and when it was looking at her, she touched one of the cups. At this point the subject was released and could choose one of the cups while the experimenter was still touching it. Regardless of its choice the subject could eat the food from the chosen cup. A total of six trials were addressed to each subject and the direction of the experimenter’s signal was counterbalanced in RLRLRL or LRLRLR order (for half of the participants the trial sequences were started with leftward touch and for the other half with rightward touch). A choice was coded when the subject ate the food from one of the cups with score 1 for the indicated and score 0 for the non-indicated location. If the subject did not make a choice within 20 seconds, it was led back to the starting point and received a score of 0.5. If the subject refused to choose three times in a row, the test was terminated. Subjects that did not make any choice during the test were regarded as “not willing to participate” and were excluded from the analysis of this test (but were included in the other tests).

Seventeen domestic ferrets, twelve wild *Mustela* hybrids and eighteen dogs completed the *Sustained touching* trials. Four wild *Mustela* hybrids were not willing to participate.

Momentary pointing (6 trials). Following the *Sustained touching* trials subjects received six additional trials with the same setup, but with the experimenter pointing to the cup without touching it (her finger stopped at 5-10 cm away from the cup) and the subject being released only after the withdrawal of the experimenters’ hand

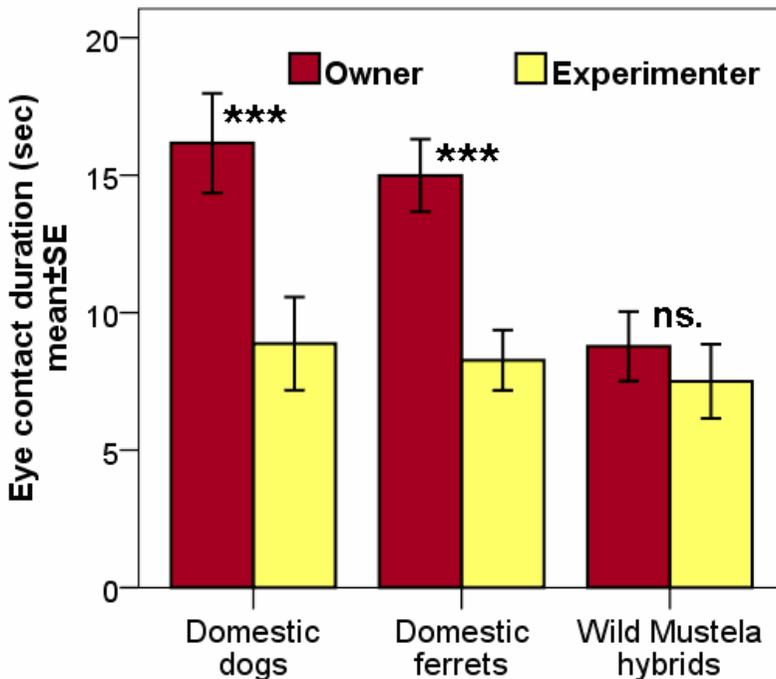
Thirteen domestic ferrets, ten wild *Mustela* hybrids and eighteen dogs completed the *Momentary pointing* trials (with four wild *Mustela* hybrids completing only part of the trials). Four domestic ferrets and six wild *Mustela* hybrids were not willing to participate.

We recorded the number of correct choices and compared it to the 50% chance level (Wilcoxon signed rank test) for the two types of directional gestures separately. The performance of domestic ferrets was compared to that of wild *Mustela* hybrids and domestic dogs with Mann-Whitney tests. Furthermore performance in the first trial was also examined (binomial test, test proportion: 0.5). All statistical tests were two-tailed.

The video protocol is available at: <http://www.cmdbase.org/web/guest/play/-/videoplayer/51>

Results and Discussion

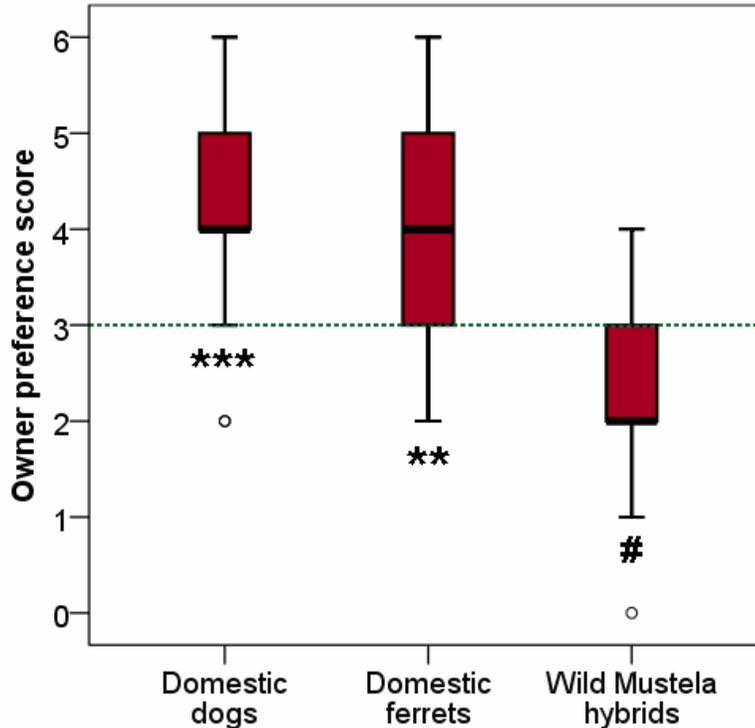
In the Tolerance of eye-contact test we found that both domestic species looked more at their owners' than at the experimenter's eyes (paired samples t-test, ferrets: $t_{(15)}=6.088$, $p<0.001$; dogs: $t_{(17)}=6.093$, $p<0.001$), while no such effect was found for the group of wild *Mustela* hybrids ($t_{(15)}=1.092$, $p=0.292$) (Figure 12). In accordance with this result, the preference for the owner (measured by subtracting the duration of looking at the experimenter's eyes from the duration of looking at the owner's eyes) was higher in the domestic ferret group than in wild *Mustela* hybrids (independent samples t-test, $t_{(30)}=0.488$, $p=0.001$), but no difference was found between domestic ferrets and dogs ($t_{(32)}=0.006$, $p=0.995$). The above difference between domestic ferrets and wild hybrids resulted from the latter group looking less at the owner's eyes ($t_{(30)}=3.572$, $p=0.001$), while no such difference was found between the two groups in case of the unfamiliar experimenter ($t_{(30)}=0.389$, $p=0.700$). Thus we may conclude that the key difference between domestic ferrets and wild *Mustela* hybrids is the lack of increased tolerance for eye contact with the owner in the latter group.



12. figure Tolerance of eye-contact. Mean duration of eye-contact during a 30 sec period while the subject was gently held by the owner or the experimenter without restricting head-movements. (***: $p<0.001$, ns.: $p>0.05$; error bars represent SD)

In the Social-preference test some of the subjects were not willing to participate or completed only part of the trials (see the *Methods* section for details), but no difference was found between groups in this respect (Fischer exact test, $p>0.1$). Both domestic ferrets and dogs chose their owners (as opposed to the experimenter) significantly more often than expected by random selection (Wilcoxon Signed Rank Test; ferrets: $T+=53.5$, $p=0.004$; dogs: $T+=143.0$, $p<0.001$), while the wild *Mustela* hybrid group displayed a marginally significant preference for the unfamiliar experimenter ($T-=38.0$, $p=0.074$) (Figure 13). Domestic ferrets, in comparison with wild hybrids, selected their owners significantly more often (Mann-Whitney

U-Test; $U=19.0$, $p=0.001$), while no difference was found between the domestic ferrets and dogs ($U=132.5$, $p=0.985$).



13. figure Number of trials with owner versus experimenter preferred out of six in total.

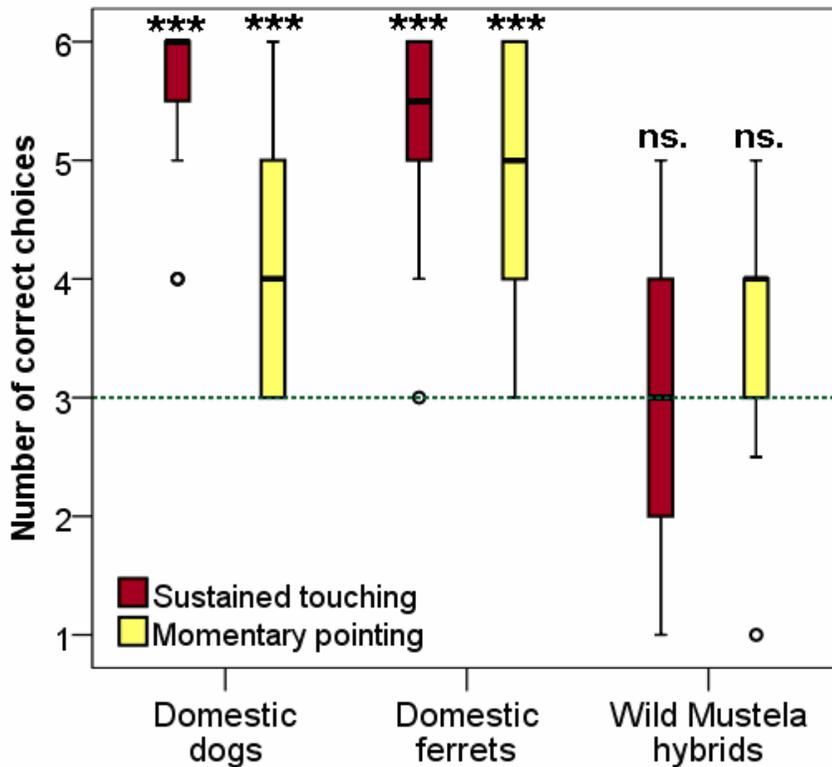
Subjects had to choose between their owners and an unfamiliar experimenter while both of them were parallelly holding a piece of food and calling the subject. Dotted line represents the chance level. (***: $p<0.001$, **: $p<0.01$, #: $p<0.1$; median, quartiles, whiskers and outliers)

It should be noted that while domestic dogs and ferrets all had female owners, some of the wild *Mustela* hybrids had male owners. No difference was found in the Tolerance of eye-contact test between wild *Mustela* with male and female owners in the duration of eye-contact with the owner ($N_1=9$, $N_2=7$, $t_{(14)}=0.849$, $p=0.409$) and with the experimenter ($t_{(14)}=0.262$, $p=0.796$). However wild *Mustela* hybrids with male owners showed higher owner preference in the Social preference task than those with female owners ($N_1=8$, $N_2=5$, $U=5.1$, $p=0.037$). This might possibly be explained by the fact that it is easier to make a distinction between a male versus a female, and suggests that wild *Mustela* hybrids were involuntarily tested in an easier version of the Social preference task. Interestingly however, despite their “advantage”, wild hybrids as a group showed lower preference towards their owners than the two domesticated groups.

Finally, in the Responsiveness to human gestures test wild *Mustela* hybrids were less willing to participate than domestic ferrets both in the *Sustained touching* (Fischer exact test, $p=0.04$) and the *Momentary pointing* (Fischer exact test, $p=0.03$) task. Furthermore those subjects in the wild *Mustela* hybrid group that did complete all 12 trials had a higher domestic ferret blood ratio ($t_{(13)}=2.12$, $p=0.05$) than those that did not.

Both domestic ferrets and dogs followed the human directional gestures above chance level in the *Sustained touching* (Wilcoxon Signed Rank Test; ferrets: $T+=120.0$, $p<0.001$; dogs: $T+=171.0$, $p<0.001$) and the *Momentary pointing* (ferrets: $T+=66$, $p=0.001$; dogs: $T+=66$,

p=0.001) conditions. Wild *Mustela* hybrids however, did not succeed in any of these tasks (touching: T+=26.5, p=0.652; pointing: T+=23, p=0.109) (Figure 14). No effect of the owners' gender could be observed in case of the wild *Mustela* hybrids (*Sustained touching*: male owner (N=8): 52.78%, female owner (N=5): 55.56%, U=23.5, p=0.343; *Momentary pointing*: male owner (N=6): 52.78%, female owner (N=4): 50.00%, U=10, p=0.999). Domestic ferrets outperformed their wild hybrid counterparts in both the *Sustained touching* (Mann-Whitney U-Test; U=15.5, p<0.001) and the *Momentary pointing* (U=20.0, p=0.015) tasks. At the same time no difference was found between the domestic ferrets and dogs in any of the two tasks (*Sustained touching*: U=114.0, p=0.231; *Momentary pointing*: U=68.5, p=0.584).



14. figure Correct choices out of six trials in the two choice situations based on directional signals. In the sustained touching trials the subject was released while the experimenter was still touching the hiding place. In the momentary pointing trials the experimenter withdraw her hand following the pointing gesture before the subject was released to make a choice. Dotted line represents chance performance. (***: p<0.001, **: p<0.01, ns.: p>0.05; median, quartiles, whiskers and outliers)

Furthermore when analyzing only the first trial (it was a *sustained touching* trial for all subjects) both domestic species succeeded in choosing the indicated cup (binomial tests, test proportion: 0.5; ferrets: p=0.001; dogs: p=0.008) while wild *Mustela* hybrids did not (p=1.0).

These findings provide striking evidence that unlike intensively socialized wild *Mustela* hybrids, domestic ferrets and dogs share some social-behavioural characteristics showing the ability to tolerate/prefer eye-contact with their caregivers, displaying preference towards their owners and reliably following human directional gestures. Furthermore it seems that subjects' willingness to participate (at least in some forms of interactions with humans) is affected by their domestication history. Dogs have already been reported to show specific behaviours towards their owners that manifests for example in increased responsiveness to the owner

compared to an unfamiliar human (Topál et al. 1998; Prato-Previde et al. 2003). The specific reaction to separation from and reunion with the human caregiver can also be observed in few months old dog puppies but is seemingly lacking in extensively socialized wolves (Topál et al. 2005). Thus similarly to dogs' other specific social skills (Miklósi et al. 2004; Hare & Tomasello 2005) one can argue that the ability of showing distinctive behaviour towards the owner also evolved during the process of domestication. Although early socialization might have an important effect on interspecific social relationships, species-specific differences in their social preference towards humans do in fact appear at a very early age in hand raised and intensively socialized dog and wolf puppies (Gácsi et al. 2005).

The results obtained from *Tolerance of eye contact* and *Social preference* tests show striking differences between domestic ferrets and wild *Mustela* hybrids in their specific responsiveness towards their caregivers. Although based on the present results we cannot decide whether the behaviour of ferrets is guided by auditory and/or visual cues, the differences found between domestic and wild individuals allow us to draw a parallel between domestic ferrets and dogs with regard to the studies comparing domestic individuals (ferrets/dogs) with their wild counterparts (*Mustela* hybrids/wolves). Our findings suggest that the owner-preference showed by domestic ferrets is a consequence of their genetic differences from the wild *Mustela* hybrids emerged during their domestication history and that behaving distinctively towards the owner may be a basic trait shared by different domestic species.

It is widely accepted that during the process of domestication dogs were selected for preferring the eye contact with humans and for exploiting this form of social interaction as a potential source of information (Miklósi et al. 2005). Propensity to make eye-contact with humans has already been shown to be an important factor in tasks where subjects have to base their choice on human communicative gestures and accounts for the failure to follow human gestural cues in the case of wolves (Miklósi et al. 2003; Gácsi et al. 2009) and apes (Mulcahy & Hedge 2012). The present findings are in line with these arguments as domestic ferrets and dogs – both showing increased tolerance of eye-contact in some sense – were equally successful in following human gestural cues while wild *Mustela* hybrids were not. It is frequently claimed that the utilization of gestural signals presupposes some cognitive skills on the part of the receiver beyond the ability to generalize from everyday communicative interaction with humans to a more controlled experimental situation. However, the fact that domestic ferrets and dogs can rely on human cueing in directing their behaviour in a choice situation is not surprising, since with appropriate human social contact and training, non-domesticated species such as monkeys (Kumashiro et al. 2002), dolphins (Herman et al. 1999), seals (Scheumann & Call 2004) and even adult wolves (Udell et al. 2008; Gácsi et al. 2009) have been shown to be able to rely on this cue in a two-way object choice test. However, subjects in the present study (contrary for example to the above mentioned ape species) did not receive formal training prior to the experiment and were not habituated to the cups containing the food reward. Similarly they did not undergo intensive experimental socialization to humans. Yet, members of the two domesticated species were successful from their first trial on, whereas members of the wild *Mustela* group were not. This provides evidence of both domestic ferrets and dogs spontaneously attending to humans and further confirms the assumption that

domestication involves genetic changes that lead to enhanced socio-cognitive abilities toward humans.

In sum the findings of this study open the door for enlarging the scope of the domestication hypothesis (Hare et al. 2002). Besides being the first one investigating human-directed socio-cognitive skills in ferrets, provides an important contribution to the recent debate (Udell et al. 2010; Miklósi & Topál 2011) over whether or not domestication could lead to the emergence of enhanced social abilities. The fact that domestic ferrets seem to be more ‘dog-like’ than ‘wild ferret-like’ regarding their social-affiliative behaviours and responsiveness to human directional gestures strongly supports the notion that (at least some of the) domestic species have acquired a set of social skills that improve their chances to survive in human communities and as a result, they share certain basic capabilities related to social cognition.

PART IV: Biological background of dogs' social cognition

In Part III. we have seen that dogs (or more broadly speaking domestic species) show human-analogue socio-cognitive skills in certain domains and thus constitute an important line of research aiming to disentangle the effects of the human environment on these behaviours. Another line of research has identified several underlying neural, hormonal and genetic mechanisms that contribute to human sociality. Special attention has been devoted to the oxytocin system (Lee et al. 2009). The central actions of oxytocin include regulating reproductive behaviour, mother-offspring attachment (Donaldson & Young 2008) and social memory (Savaskan et al. 2008). Moreover, the oxytocin system is involved in several neurological disorders such as autism, depression and social anxieties (Hollander et al. 2007). In this chapter we combine these two lines of research and examine the effect of single nucleotide polymorphisms (SNPs) in the oxytocin receptor (OXTR) gene as well as intranasal oxytocin (OT) administration on certain aspects of dog social behaviour.

Gene × behaviour associations⁶

Background

Due to their particular domestication history and the special socio-cognitive skills, dogs became a widely used model species in behavioural genetics (Hejjas et al. 2007; Kubinyi et al. 2012). Dogs' special bond to humans, their complex human-analogue social behaviour and the fact that the dog genome has been sequenced (Kirkness et al. 2003) make them ideal candidates for this kind of research. A further advantage is that several human psychiatric disorders have an analogue in dogs (Overall 2000; Parker et al. 2010), while in the traditionally used rodent models these conditions need to be induced artificially.

The oxytocin system is evolutionarily conserved, both the hormone and its receptor are present in mammals and other taxa (Gimpl & Fahrenholz 2001; Donaldson & Young 2008). However variations caused by genetic polymorphisms might modulate the function of this complex system (e.g. humans: Kumsta & Heinrichs, 2012; prairie voles: McGraw et al. 2012). Polymorphisms in the oxytocin receptor (OXTR) gene have been shown to influence human social behaviours such as attachment (Gillath et al. 2008; Chen et al. 2011) or empathy (Rodrigues et al. 2009).

It has already been shown that the similarity between the human and the dog OXTR gene is high (Marx et al. 2011). The human peptide is composed of 389 amino acids, while the dog version contains 384 amino acids. Twenty-six locations contain different amino acids, but eight of these are similar in chemical properties (polarity, acidity).

So far no information on the dog OXTR gene polymorphisms are available thus the role of these polymorphisms in regulating behaviour is also unexplored. Our aim in the current exploratory study was search for preliminary evidence of possible associations between human-

⁶ This chapter is based on: **Kis, A., Bence, M., Lakatos, G., Pergel, E., Turcsán, B., Pluijmakers, J., Vas, J., Elek, Z., Brúder, I., Földi, L., Sasvári-Székely, M., Miklósi, Á., Rónai, Z., Kubinyi, E.** (2014). Oxytocin receptor gene polymorphisms are associated with human directed social behavior in dogs (*Canis familiaris*). *PLoS ONE*, 9(1) e83993

directed social behaviour and OXTR gene polymorphisms in two dog breeds (German Shepherds and Border Collies).

Methods

Our subjects were 104 privately owned adult (>1 year; mean age \pm SD: 3.88 \pm 2.55) German Shepherd dogs (58 males, 46 females) and 103 adult (>1 year; mean age \pm SD: 4.28 \pm 2.74) Border Collies (46 males, 57 females). None of the subjects were closely related, i.e. littermate and parent-offspring relationships were excluded.

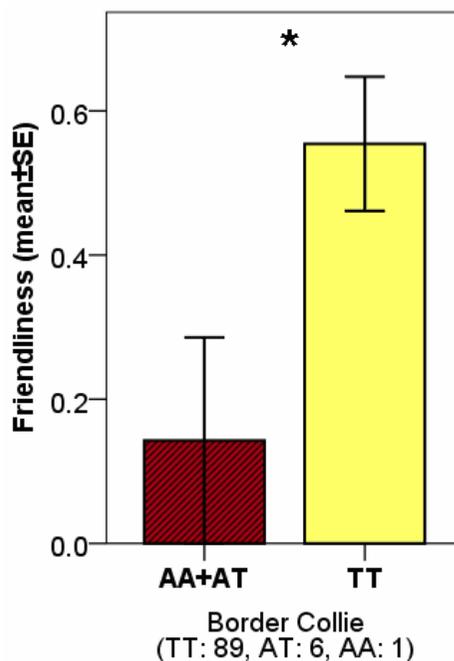
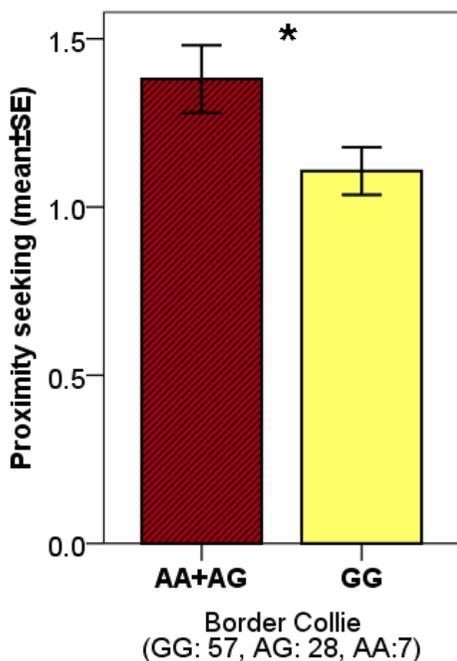
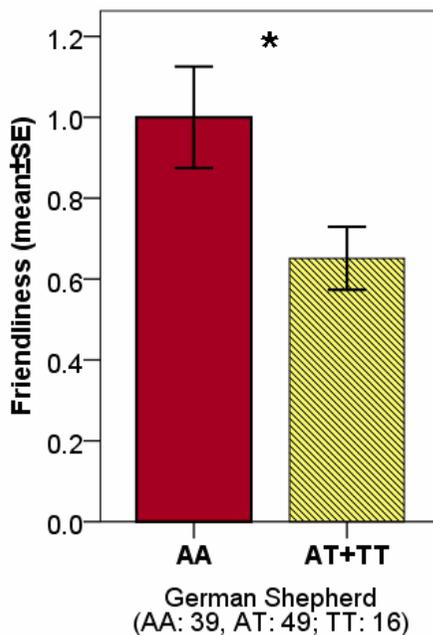
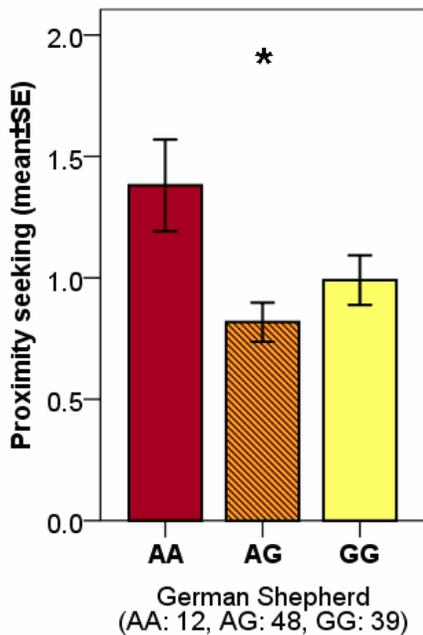
Phenotyping was carried out by a self-developed test that consisted of five episodes and measured four behavioural scales: Proximity seeking, Reaction to separation from owner, Friendliness, Looking at humans (for detailed description of the test series as well as the steps of data processing see Appendix 1). Subjects were genotyped for three newly described OXTR SNPs positioned in the 3' and 5' UTR regulatory regions (for the description of these SNPs see Appendix 2). Gene \times behaviour associations were tested with ANOVA or independent samples t-test depending on the allele frequencies. The analyses were conducted for German Shepherds and Border Collies separately because there was a significant difference in both the behaviour (see Appendix 1) and the allele frequencies (see Appendix 2) of the two breeds. Rare homozygote genotypes were grouped together with heterozygotes for the present analysis. As the expected effect sizes for the contribution of one SNP to a behavioural trait were relatively small, similarly to other (human) gene \times behaviour studies (e.g. Gillath et al. 2008; Rodrigues et al. 2009) the statistical tests were not corrected for multiple comparison.

Results and Discussion

The -212AG polymorphism was associated with Proximity seeking both in case of German Shepherds ($F=4.030$, $p=0.021$) and Border Collies ($t=2.282$, $p=0.025$); carrying the G allele, was associated with lower proximity seeking in both breeds (Figure 15). Associations with the other three behavioural scales were not significant (all $p>0.05$, Table 2).

The rs8679684 polymorphism was associated with Friendliness both in case of German Shepherds ($t=2.570$, $p=0.012$) and Border Collies ($t=2.412$, $p=0.033$). However an opposite trend could be observed in the two breeds. In German Shepherds carriers of the A allele, as opposed to the T allele, achieved higher scores on the Friendliness scale, while in Border Collies individuals carrying the A allele were less friendly (Figure 16). Associations with the other three behavioural scales were not significant (all $p>0.05$, Table 2).

As a result of linkage disequilibrium (see Appendix 2) the 19131AG polymorphism, similarly to the rs8679684 SNP, was associated with Friendliness both in case of German Shepherds ($t=2.724$, $p=0.008$) and Border Collies ($t=2.800$, $p=0.013$). The presence of the A allele, as opposed to the G allele was associated with higher Friendliness scores in German Shepherds and lower Friendliness scores in Border Collies. Associations with the other three behavioural scales were not significant (all $p>0.05$, Table 2).



15. figure Proximity seeking score mean differences between the different -212AG genotypes in German Shepherds (a) and Border Collies (b). Sample sizes for each genotype group are provided in parenthesis. *: $p < 0.05$

16. figure Friendliness score mean differences between the different rs8679684 genotypes in German Shepherds (a) and Border Collies (b).

*: $p < 0.05$

In this study we provide the first evidence that polymorphisms in the OXTR gene are related to human directed social behaviour in dogs. Although we do not, at this point, have any information about the intermediary (cellular and molecular) mechanisms directly involved in the regulation of the behaviours we observed, the indirect gene \times behaviour connection is in line with previous findings in humans (Lucht et al. 2009; Saphire-Bernstein et al. 2011). Thus

these results further extend the role of the dog as a model species in behaviour genetic research (Parker & Ostrander 2005) by possibly aiding future research leading to the understanding and treatment of human social disorders. However we also note, that due to the low effect sizes that are characteristic of these gene \times behaviour studies (Munafò 2009; Chabris et al. 2012) our results need to be replicated before more specific conclusions can be drawn.

	German Shepherds			Border Collies		
	<i>-212AG</i>	<i>rs8679684</i>	<i>19131AG</i>	<i>-212AG</i>	<i>rs8679684</i>	<i>19131AG</i>
Proximity seeking	F=4.030 *	t=0.641 ns.	t=0.931 ns.	t=2.282 *	t=1.119 ns.	t=0.964 ns.
Reaction to separation from owner	F=1.083 ns.	t=0.096 ns.	t=0.147 ns.	t=1.581 ns.	t=0.738 ns.	t=0.473 ns.
Friendliness	F=0.171 ns.	t=2.570 *	t=2.724 **	t=0.739 ns.	t=2.412 *	t=2.800 *
Looking at humans	F=0.710 ns.	t=0.140 ns.	t=0.022 ns.	t=1.514 ns.	t=1.242 ns.	t=1.514 ns.

2. table Associations of the OXTR SNPs with the behavioural scales.

**.: $p < 0.01$, *: $p < 0.05$, ns.: $p > 0.05$

The oxytocin system is most often related to prosocial behaviours (Yamasue et al. 2012) and trust (Baumgartner et al. 2008). Although it is hard to draw a parallel between the behavioural measurements in the present study and for example the computerized trust games that are most often used with humans, our results are in accordance with previous findings as we found that polymorphisms in the OXTR gene had an effect on the Proximity seeking and Friendliness of dogs.

We should note, however, that the polymorphisms related to Friendliness had an opposite effect on German Shepherds and Border Collies, suggesting that other genetic and cellular mechanisms (unexplored in the present study) might play a role in the regulation of this behaviour besides our candidate gene. Recent accounts in the human literature have cautioned about the individual (e.g. motivation or anxiety of the subjects) and conditional (e.g. contextual) differences in the effects of oxytocin on social behaviour (Bartz et al. 2011) suggesting that it would be erroneous to assume that oxytocin broadly and invariantly improves social cognition. Our results somewhat parallel these ideas in that we also found that in dogs the influence of a SNP in the OXTR gene on Friendliness towards humans is conditional to a breed effect.

Polymorphisms in the OXTR gene have been shown to be related to security/insecurity of mother-infant attachment in humans (Chen et al. 2011) that manifests in behaviours such as approach and physical contact towards the caregiver in reunion episodes. Our results are in agreement with this finding as in dogs an OXTR gene polymorphism was related to Proximity seeking; on the other hand we did not find any effect on the Reaction to separation from the owner.

It has also been shown that oxytocin increases looking at the eye-region of faces in humans (Guastella et al. 2008a), and based on this finding one could expect a general relationship between the oxytocin system and looking at the eyes/face of humans. However other studies

have questioned if such a relationship exists (Lischke et al. 2012) and we also could not find any effect of OXTR gene polymorphisms on how much dogs look into the face of humans. We should note, however, that the test used in the present study consisted of problem solving situations when the dogs had a chance to look back at their owners and/or the experimenter, while in the human studies (Guastella et al. 2008a; Lischke et al. 2012) subjects were presented with computerized stimuli on a monitor. This latter setup has also been used with dogs (Hernádi et al. under review), and in this case it has been found that intranasally administered oxytocin decreased looking at the eye region.

This is the first behavioural genetic evidence for OXTR's previously suggested (Beetz et al. 2012) involvement in interspecific (dog-human) interactions. Further studies should replicate and extend these preliminary findings, as well as reveal the mediating molecular mechanisms. As the oxytocin system has been implicated in several human neurological disorders (Hollander et al. 2007), the present results – together with the fact that the dog is a natural model of complex human illnesses (Overall 2000) – open up the possibility for future research of the genetic background of certain social disorders.

The effect of intranasal oxytocin on behaviour⁷

Background

As introduced in the previous chapter oxytocin is specifically involved in the regulation of human and non-human social cognition (Yamasue et al. 2012) and we have also found some behavioural genetic indications that the oxytocin system is involved in the regulation of human-directed social behaviours in dogs. We have seen that an increasing body of evidence supports the notion that, in spite of their phylogenetic distance, dogs and humans (infants), often show comparable socio-cognitive functioning at the behavioural level. These comparable socio-cognitive skills include for example “moral-like” behaviours such as aversion to inequity (Range et al. 2009, 2012; but see: Horowitz 2012), reputation formation based on third party interactions (Kundey et al. 2011; Marshall-Pescini et al. 2011; Freidin et al. 2013) and sensitivity to being watched (Bräuer et al. 2004; Schwab & Huber 2006; Kaminski et al. 2012b). Dog also show a sensitivity to human ostensive-communicative cues that is similar to human infants' (Topál et al. 2009b; Téglás et al. 2012; Kaminski et al. 2012a). Furthermore dogs have the same personality dimensions as humans, which are consistent across time and situations (Gosling et al. 2003; Jones & Gosling 2005; Turcsán et al. 2012). It has also been shown that some degree of comparability exists between dogs and humans in “dispositional optimism”, a characteristic behavioural trait which in humans is often conceptualized as positive expectation bias. For example, tendency to form “pessimistic ” judgements are associated with increased level of depressive symptoms in humans (Strunk et al. 2006) and separation related behaviour problems in dogs (Mendl et al. 2010). Furthermore recent findings suggest an association between oxytocin and self-assessed psychological well-being in humans (William et al. 2011). Optimism has also long been investigated due to its role in human health and well-being (Scheier & Carver 1992) as expectancy biases are known to be influenced both positively and negatively by people's current mood (Carver et al. 2010). Recent research has

⁷ This chapter is based on: **Kis, A., Hernádi, A., Kanizsár, O., Gácsi, M., Topál, J. (under revision).** Oxytocin induces an ‘optimistic’ cognitive bias in dogs (*Canis familiaris*). *Hormones and Behavior*

linked such psychological resources to the oxytocin system (Saphire-Bernstein et al. 2011), although the results are still controversial (Cornelis et al. 2012).

In the current study we combine these lines of research and investigate the effects of intranasally administered oxytocin on “optimistic ” cognitive bias (Harding et al. 2004) in dogs. As previous research (e.g. Topál et al., 2009; see also Part III.) has shown that the social-communicative nature of the task (whether the human experimenter addresses the subjects and makes eye-contact with them) can greatly influence dogs’ performance, we decided to test the effect of oxytocin in both communicative and non-communicative test contexts.

Methods

Subjects

Sixty-four adult (>1 year) pet dogs (28 males, 36 females; mean age±SD: 4.44±2.67 years) from various breeds were tested in four experimental conditions: subjects received oxytocin (OT) or placebo (PL) pre-treatment in communicative (Com) or non-communicative (NCom) contexts (N=16 in each).

Procedure

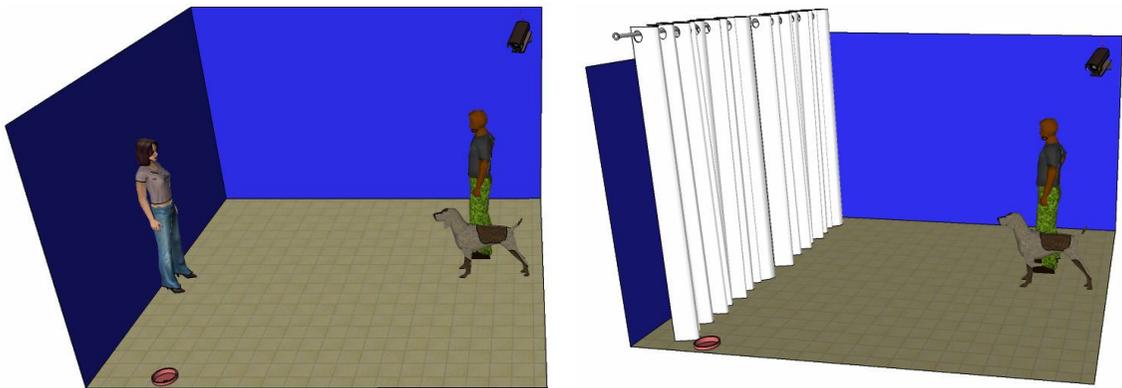
The training phase was identical for all subjects and was based on the procedure developed by Mendl et al. (2010); see Figure 17/a. (For a comparison of different Cognitive Bias procedures see Appendix 3.) The dog was held on leash by the owner at a 3 m distance from the two possible hiding locations placed on the left and right side of the room 2 m apart from each other. The experimenter positioned herself facing the subject, established eye-contact with the dog and addressed it (dog’s name + “Look!”) and placed the food bowl to either of the two locations in a fixed semi-random order so that at the positive side the bowl always contained a food reward while at the negative side it was always empty. The positive and negative side (left/right) was counterbalanced across subjects. The dog was allowed to approach the food bowl in every trial, while the experimenter was looking straight ahead without maintaining eye contact with the dog, and the latency of approach was noted. Dogs were deemed to have learnt an association between bowl location and food reward when – for the preceding five positive trials and the preceding five negative trials – the longest latency to reach the positive location was shorter than any of the latencies to reach the negative location (Wilcoxon Test, $p=0.025$).

After having reached this learning criterion, half of the subjects received a single intranasal dose of 12 IU oxytocin (Syntocinon-Spray, Novartis) (OT, N=32) or placebo, isotonic natriumchlorid 0.9% solution (PL, N=32). (In order to ensure that intranasal OT administration had the physiological effect that could be expected based on the human literature ECG measures (HR & HRV) were taken on a sub-sample of dogs in separate sessions; see Appendix 4.) Then, after a 40-minute waiting period (that is presumed to be necessary for the central oxytocin levels to reach a plateau; Born et al., 2002) dogs participated in a 9-trial re-training phase that, in case of the communicative context, was identical to the training trials, while in the non-communicative context the experimenter was hidden behind a curtain and thus provided no communicative cues (Figure 17/b). (Dogs’ behaviour during the re-training was not included in the analysis, the purpose of this phase was merely to ensure that subjects remembered which location was the positive and the negative one. The inclusion of this re-training phase was necessary because our pilot data showed that dogs’ latency to reach the food

bowl did not differ between the positive/negative sides after a 40 minutes delay that followed the training.)

The test phase consisted of a negative, a positive and an ambivalent (during which the baited bowl was placed halfway between the positive and negative locations) trial. The trials were presented in fixed order administered in the same Com / NCom context as described for the re-training. Both the training and test phases were videotaped.

Although one could argue that dogs in this situation can possibly smell whether there is food in the bowl, previous research (e.g. Lakatos et al., 2011) indicates that in similar setups dogs are not able to choose the baited cup based on odour cues alone. (This is further supported by the fact that our subjects did not differentiate in their latency to reach the positive versus negative location (paired samples t-test, $t_{(65)}=0.553$, $p=0.582$) in their first training trials.)



a) b)
17. figure Schematic drawing of the Cognitive Bias test setup in the Communicative (a) and Non-Communicative (b) contexts

Data analysis

Training phase. Mean latency to approach the positive and negative locations was calculated for each subject based on the last five positive and the last five negative trials. A Generalized Estimating Equation (GEE) model was used to confirm the effect of location (positive vs. negative; within subject factor) on the latency to approach the bowl and to test the possible differences among the four condition groups (between subject factor).

Test phase. A GEE was used to test the differences between the latency to approach the positive / negative location (within subject factor) and the effect of test context (Com vs. NCom; between subject factor) as well as the effect of pretreatment (OT vs. PL, between subject factor). Moreover, in order to assess subjects' judgement bias in the ambivalent trials, a Positive Expectancy Score (PES) was calculated for each subject from the latency to approach the negative, positive and ambivalent locations according to the following formula (modified from Mendl et al., 2010):

$$100 - \frac{(\text{latency to reach ambivalent location} - \text{latency to reach positive location}) * 100}{\text{latency to reach negative location} - \text{latency to reach positive location}}$$

A General Linear Model (GLM) was used to test the effect of test context (Com or NCom; between subject factor) as well as the effect of pretreatment (OT or PL; between subject factor) on PES. Planned pairwise comparisons (independent samples t-tests) were carried out to assess

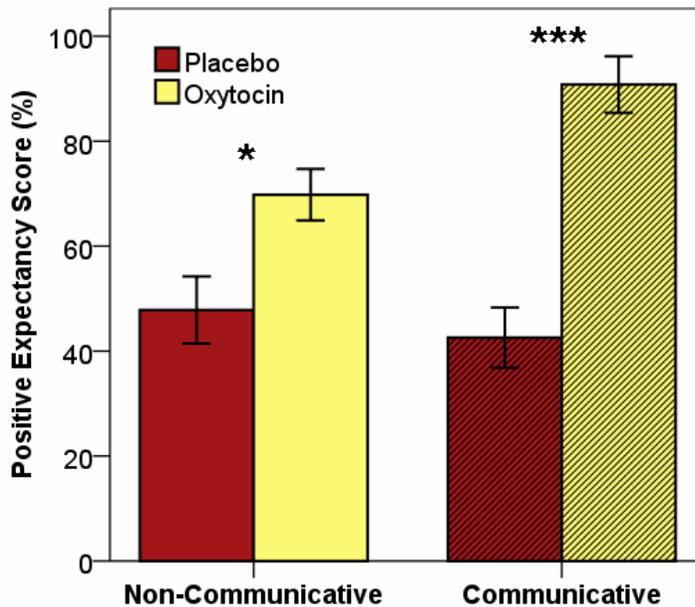
the effect of OT versus PL pretreatment in both the Com and NCom contexts; as well as to assess the effects of Com versus NCom test contexts for both OT and PL pretreated dogs.

Results and Discussion

The GEE (Generalized Estimating Equation) analysis revealed that by the end of the training phase there was a consistent difference in the latency to approach the positive versus negative location (with a shorter latency for the positive location; $\chi^2=55.215$, $p<0.001$) while the four condition groups did not differ from each other ($\chi^2=3.827$, $p=0.281$) and there was no significant group \times location interaction ($\chi^2=3.123$, $p=0.373$).

During the test phase a similar difference was found between the positive and negative locations (GEE, $\chi^2=35.664$, $p<0.001$). However, dogs in the non-communicative context showed higher latencies ($\chi^2=10.938$, $p=0.001$) irrespective of PL/OT pretreatment ($\chi^2=0.386$, $p=0.534$). This was true for both the positive and negative locations as no significant interactions were found (all $p>0.05$). More importantly, dogs receiving OT pretreatment achieved a higher Positive Expectancy Score (PES), than dogs receiving PL pretreatment (GLM, $F=38.818$, $p<0.001$) and this difference was more pronounced in the communicative context as reflected in a significant pretreatment \times context interaction ($F=5.434$, $p=0.023$, Figure 18). There was no main effect of Com/NCom contexts ($F=1.952$, $p=0.167$).

Planned pairwise comparisons confirmed these results as OT pretreated dogs achieved higher PES both in the Com ($t_{(30)}=6.118$, $p<0.001$) and in the NCom ($t_{(30)}=2.729$, $p=0.011$) contexts. Furthermore, OT pretreated dogs achieved a higher PES in the Com than in the NCom context ($t_{(30)}=2.884$, $p=0.007$), whereas PL pretreated dogs did not show a context dependent difference ($t_{(30)}=0.612$, $p=0.545$).



18. figure The Positive Expectancy Scores (PES) of dogs in the non-communicative and social-communicative versions of the cognitive bias task after placebo / oxytocin pretreatment (mean \pm SE). A higher PES indicates a reaction to the ambivalent location that is more similar to the reaction to the positive than to the negative location. *: $p<0.05$, ***: $p<0.001$

This study presents new information in the growing debate over whether oxytocin modulates optimistic bias in humans (Saphire-Bernstein et al. 2011; Cornelis et al. 2012) or in nonhuman animals. Our results provide the first evidence suggesting that oxytocin induces positive expectations in dogs. Recent research has provided an increasingly coherent picture of the involvement of oxytocin in the regulation of human and non-human social behaviour phenomena (such as trust – Kosfeld et al. (2005) and generosity – Barraza et al. (2011) or social memory – Ferguson et al. (2002; Guastella et al. (2008b)), and in our study the judgement bias in dogs about ambivalent stimuli also appears to be modulated by the social-communicative nature of the task context. These findings extend our previous knowledge about the role of oxytocin in positive emotions and welfare (Mitsui et al. 2011) and reveal an interesting parallel between dogs and humans with regard to the connectedness between the oxytocin system and positive expectation bias. Human optimism as well as the “optimistic/pessimistic” cognitive bias in animal models have been linked to mental health (Scheier & Carver 1985, 1987) and behavioural problems (such as separation anxiety (Mendl et al. 2010)), therefore our results have potential applied and clinical relevance as well. We note, however, that further studies should determine how other factors, such as baseline optimism of the subjects and/or polymorphisms in the OXTR gene, modulate the effect that we have found.

Previous research has shown that the dog is a promising model species to study human psychiatric conditions (Overall 2000) as well as the genetic background of certain illnesses (Parker et al. 2010). The present results extend these notions by showing that a similar neuro-hormonal mechanism (the oxytocin system) might be responsible for a crucial psychological resource, the optimistic judgement of ambivalent stimuli. Importantly, in addition to ample evidence on the role of oxytocin in regulating social behaviour in humans and rodents (Donaldson & Young 2008), this is the first evidence of the effect of intranasally administered oxytocin on dog behaviour, and thus our results open up the way for further research to use the dog as a model of human socio-cognitive competences (Miklósi & Topál 2013) at the neurohormonal level as well.

PART V: Dog as a model for social robotics⁸

Background

A relatively new approach that has also been suggested to use dogs as model species is social robotics (Miklósi & Gácsi 2012). Social robots are or will soon be present in our society fulfilling a wide variety of social roles: e.g. guided tours in a museum (Nourbakhsh 1999), reception and tourist information (Gockley et al. 2005), education (Billard 2003), helping and looking after elderly people (Pineau 2003), companion and play-mate (Arkin et al. 2003), assistant (Severinson-Eklundh et al. 2003) etc. Thus these robots need to interact with humans in a way that is more or less natural for them and the least disturbing possible. In order to do that it is essential for the robot to act in accordance with the given social situation and show relevant emotions (Bartneck et al. 2004; Leite et al. 2008). In robotics, up to now human behaviour and facial expressions have constituted the basis for developing autonomous expressive behaviours in artificial agents (e.g. Cañamero & Fredslund 2000; Bartneck 2001; Kätsyri et al. 2003). The ability to converse is also regarded as one of the main design requirements (e.g. Li et al. 2011), however, the communication of emotional states by non-linguistic behaviour also plays an important role in humans. A well-known social robot, Kismet, for example displayed a range of emotive expressions not exclusively through facial expressions but also using body posture and gaze direction (Breazeal 2002), as well as quality of voice (Breazeal 2003).

The uncanny valley hypothesis (Mori 1970) claims that the more human-like a robot is, the more familiar it seems to us until a specific level of familiarity at which subtle imperfections make the robot seem eerie (e.g. MacDorman et al. 2009). This “valley” manifests just before total human likeness and applies to both physical appearance and behaviour, suggesting that humanoid or android robots might not always be ideal for interactions with humans (but see MacDorman & Ishiguro 2006).

Considering the abilities and limitations of most present-day social agents, it seems that in human-robot social interactions presenting relevant human-like facial expressions and comprehending the human’s facial expressions pose insolvable difficulties for the robots. Additionally, most social robots do not need verbal abilities or a human-like face to fit their original function (e.g. Pineau 2003; Severinson-Eklundh et al. 2003). Although facial expressions provide important cues for communicating emotional states, based on mammalian homologies humans possess an evolutionarily more ancient behavioural system that expresses changes in the inner state by means of the whole body. Furthermore recent studies support the claim that humans recognize/identify some basic emotional states based on simple behavioural displays in several animal species (Morris et al. 2000; Waller et al. 2007). However, in these cases human subjects tend to capitalize also on the context of the observed expressive behaviours (e.g. Meeren et al. 2005; Aviezer et al. 2009).

Based on the above considerations, we suggest viewing the human-robot interaction as an interspecific interaction and propose using a non-human species, the dog, as a potential natural

⁸ This chapter is based on: **Gácsi, M., Kis, A., Faragó, T., Janiak, M., Muszyński, R., Miklósi, Á. (in prep)**. Humans attribute emotions to a robot that shows simple behavioural patterns borrowed from dog behaviour.

model for developing and testing social robots and human-robot interactions (see in detail: Miklósi & Gácsi 2012). As we have seen in previous chapters due to the shared social environment of dogs and humans in the course of domestication, the social competence between humans and dogs is claimed to be exceptional (Topál et al. 2009a). Dogs can successfully communicate and cooperate with humans, and show social behaviours that humans can easily understand without massive prior learning. Dogs are able to develop individual attachment relationships with humans even in adulthood (Gácsi et al. 2001), have different personalities resembling human personality types (Gosling et al. 2003; Kubinyi et al. 2009), and most importantly, their owners tend to attribute complex emotions to them (Morris et al. 2008; Horowitz 2009; Hecht et al. 2012). It is worth to mention that most probably other domestic species also possess similar socio-cognitive skills (see e.g. Part III), however much less information is available about their behaviour compared to dogs'.

The dog has already been successfully applied as the prototype of nonhuman companions in human-robot interaction research (Kovács et al. 2009; Syrdal et al. 2010). Social robots are designed to actively interact with humans and, similarly to dogs, they need to fulfil double criteria: 1) successful performance of the actions necessary for their specific function, and 2) showing believable social/communicative abilities during interactions with the human users. During the process of domestication the dog adapted to the human environment and acquired or expanded the competencies necessary to fulfil the second criteria. With respect to the functions, dog breeds were selected to fit specific purposes to assist human activities. It seems that, in a broad sense, social robots and dogs play rather similar roles in the human environment.

Humans' success in identifying dogs' expressive behaviours and their tendency to credit dogs' inner states based on short action sequences viewed on video clips seems to be irrespective of their previous experiences with dogs (Tami & Gallagher 2009). Considering the acoustic modality, Pongrácz et al. (2005) found that most types of dog barks bear a very strong emotional content for human listeners. Moreover, humans with different levels of experience with dogs described the emotional content of the bark sequences quite similarly (Pongrácz et al. 2006). Due to the different modalities and the redundant nature of dogs' expressive behaviours (vocalization, movements, posture, signallers such as ear set, tail carriage, and change in size such as crouching or piloerection of the hair, etc.) (e.g. Fox 1971), we suggest that it is possible to extract relevant behavioural actions from this rich repertoire for social robots of different embodiments and functions.

In this study we have investigated whether people tend to attribute corresponding inner states to a robot displaying behaviours based on dogs' expressive behaviours, when viewing short video records. In order to avoid the influence of the social context that has been shown to play a crucial role in interpreting emotional states (e.g. Carroll & Russell 1996), our stimuli were recorded in a neutral laboratory environment. The PeopleBot robot used in this experiment had a markedly different embodiment compared to dog morphology (see Figure 19), moreover it had a clearly mechanistic appearance lacking a human-like face and verbal abilities. We hypothesised that observing and describing pet dogs' behaviour elements in simple social situations would allow us to extract the typical behaviour patterns which can help humans to recognize the robotic agent's inner state during interactions. Therefore, as a first step, in this study we utilized some relevant dog behaviours to express inner states in the robot.

We investigated the extent to which people can recognize the same inner states in the case of a robot and a dog when they observe both individuals acting on short video records that lack any social context. We also analysed the effect of the subjects' experiences with dogs and their gender on the recognition success.

Methods

Subjects

Our human subjects (N=81) were 53 females and 28 males, from an age range of 18-26 years. They were voluntaries recruited from university students of different majors. From these subjects 39 owned a dog, while the remaining 42 did not have a dog. Subjects watched the videos in one of six quasi-random orders (half of them starting with the robot videos while the other half starting with the dog videos and with the order of emotions randomly distributed within the dog and the robot blocks) and completed the questionnaire in small groups. They were blind to the purpose and hypothesis of the study, and the female experimenter did not give them any specific information during the test.

Robot and dog

The robot used in this study was a PeopleBot research platform manufactured by the MobileRobots company (Figure 19/a). It was built on a robust differential-drive P3-DX wheeled mobile platform which was able to turn/spin in-place and navigate inside indoor environment. The robot base had a chest-level extension with a touch-screen mounted on its top. The PeopleBot could not alter its body posture or its size. The monitor mounted on the platform could be considered as a head in the sense that it had a front and a back side (so it could indicate orientation), but it could not be moved independently from the body, and had no face or eyes. Two arms were fitted on the sides of the 'body'. One of them was a robotic arm (with 5 degrees of freedom) designed at the Wroclaw University of Technology. It consisted of 2 links and a hand formed of four fingers. A non-movable arm mock-up was mounted on the other side of the "body". On account of another experiment white gloves were fixed on the hands. The robot was able to emit pre-recorded sounds.

During the video recordings the robot was remotely controlled by a human through a dedicated remote operator interface which enabled simultaneous control of the robot base and the arm movements. Robot control system consisted of an efficient industrial PC computer running under Ubuntu Linux with real time Xenomai (<http://www.xenomai.org>), the Player/Stage communication framework (<http://playerstage.sourceforge.net/>) infrastructure and software implementing robot control algorithm.

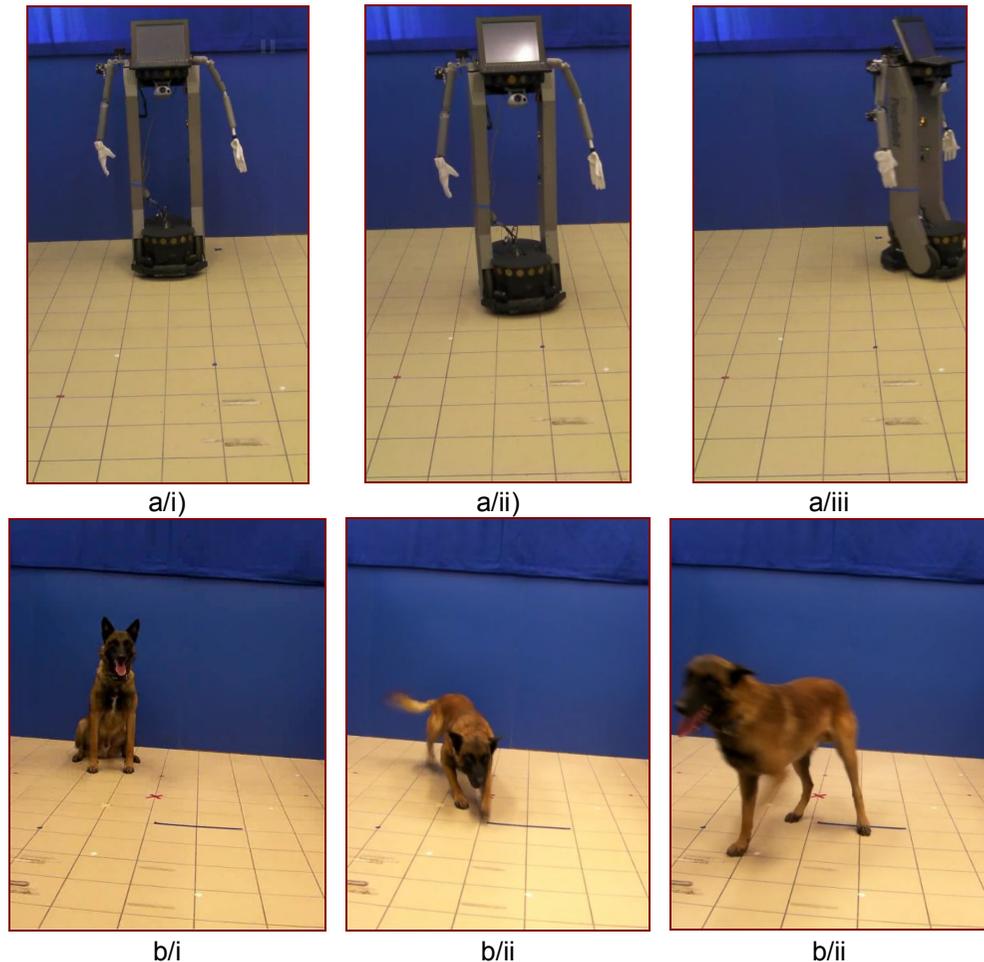
The dog acting on the videos was a 3-year-old male trained Belgian malinois that was able to display specific behaviour actions responding to human visual signals (Figure 19/b).

Establishment of the emotional behaviours for the robot

Based on a meta-analysis of previous studies (see below) we described dogs' emotional behaviours in both visual and acoustic modalities in simple social situations. We prepared a detailed list of the relevant behaviours for four basic emotional states; joy, sadness, anger, fear (Ekman 1992), and for an additional neutral state. We derived emotional behaviour from observations in the following contexts:

(1) Joy: "greeting the owner" and "going for a walk" (Topál et al. 1998; Pongrácz et al. 2005; Konok et al. 2011);

- (2) Anger: “threatening stranger” situation (Vas et al. 2005; Pongrácz et al. 2011);
- (3) Fear: “threatening stranger” situation (Klausz et al. 2009; 2014);
- (4) Sadness: “separation from owner” situation (Topál et al. 1998; Pongrácz et al. 2011);
- (5) Neutral: “mobile owner” task (Faragó et al. 2014a).



19. figure Screenshots from the beginning (i), middle (ii) and end (iii) of a robot (a) and dog (b) video stimuli depicting the emotion fear

Preparation of the video material

We prepared 5-5 short video clips with the robot and the dog, on which the actors displayed the corresponding emotional and neutral behaviours (duration: robot: 9–14 sec; dog: 8–15 sec).

Both the actions of the dog and the robot were recorded from the viewpoint of an observing human in the same laboratory, so that the acting dog and robot seemed to react to the viewer. The lack of any environmental cues excluded the possibility that the viewers deduced the inner state of the robot/dog from the context.

For the recording of the dog clips the trainer controlled the dog’s actions from behind the camera, so the dog reacted to the trainer’s signals in a way that he showed the expressive behaviours towards the camera. In case of the robot, the actions were adjusted to the limitations of its embodiment. Due to the constraints of the recording context we could not apply each behaviour element for the dog either (e.g. the dog could not fully approach the trainer in case of the joy clip that was to be based on a greeting situation).

The original sound of the robot (R2D2 like short chirps) was modified in a way that their acoustic parameters followed the Morton rules (Morton 1977) similarly to dog vocalizations (Pongrácz et al. 2006; Faragó et al. 2014b): the aggressive sound was low pitched, noisy and fast pulsing, the joyful sound had raised pitch, was less noisy and was fast pulsing, and the sad sound was elongated, slow pulsing, moderately noisy with a decreasing pitch. In case of “sadness” the voice of another dog was dubbed onto the recording, in the other two situations the voice was produced by the stimulus dog. In the case of fear and neutral clips no sound was applied. The video clips were uncut, and varied in length depending on the actions and speed of the dog and the robot.

In Table 3 we summarize the major behaviours we could apply on the videos without describing subtle movements and dynamics. As an example, Figure 19 illustrates three phases of the emotional behaviour for the emotional state of fear both in the robot and the dog.

	Dog behaviour	Robot behaviour	Vocalization in both dog and robot
JOY	approaches	approaches	high-pitched, tonal, staccato
	wags his tail	lifts one arm, moves fingers	
	sidles	partly spins	
FEAR	approaches crawling	approaches slowly	–
	hanging ears, licks lips	backs	
	turns, goes away	turns away, goes away	
SADNESS	sits down	backs	low-pitched, moderately noisy, long-drawn
	lies down	turns away	
	lays his head down	lets its arm down	
ANGER	stays motionless	stays motionless	low-pitched, noisy, loud, staccato
	approaches (lying)	approaches	
	wags his tail	moves its arm high	
NEUTRAL	moves head up and down dynamically (barking), shows teeth	swings arm several times	–
	turns toward the viewer	turns toward the viewer	
	approaches	approaches	
	stops	stops	

3. table List of the behaviours presented from the viewer’s aspect for the different emotional states on the videos.

Questionnaire

Human subjects’ interpretation of the actions of the robot and the dog as expressive behaviours was evaluated using a questionnaire consisting of an open-ended and a multiple choice part. All subjects watched the 10 video clips in a row out of which the first 5 showed either the robot or the dog (counterbalanced across subjects). Both the robot and the dog video clips were played in one of six random orders (the order within the robot and the dog blocks was always different).

Subjects watched the whole series of the 10 video clips twice. During the first viewing they were asked to complete the open-ended questionnaire and on the second occasion, when they were presented with the same 10 video clips in the same order, subjects had to answer multiple choice questions. In both cases subjects had to evaluate the records one by one, watching each video clip presentation separately.

For the open-ended questions the subjects did not receive instructions about what they would see, instead they had to describe their impressions freely. The instructions to the open-ended questions were as follows: “*In the following you will see ten short videos. Please, write down briefly what is happening on each video!*” This way, at the beginning of the experiment we did not reveal that the videos were designed to reflect emotional states.

In the case of the multiple choice questions subjects could choose from five possibilities; the list of the 5 emotional states including “neutral”. The instruction for this part was as follows: “*Please, choose from the following inner states the one which best describes the video!*” In addition subjects were asked to give a 0-4 certainty score for their choice.

Data analysis

Open-ended questions. We scored the answers for the open-ended questions depending on how directly they referred to some emotional/mental state. The subject received:

- 0 points if s/he gave no answer;
- 1 point if s/he wrote a formal description of the observed behaviour (e.g. comes closer);
- 2 points if s/he indicated some contextual behaviour (e.g. greets);
- 3 points if s/he mentioned a behaviour that indicated some inner state (e.g. threatens sy);
- 4 points if s/he named an inner state explicitly (e.g. feels joy).

Inter-observer agreement (Cohen’s kappa) for the categorisation, calculated from the double scoring of six questionnaires (altogether 60 questions) was almost perfect: 0.84 (Landis & Koch 1977).

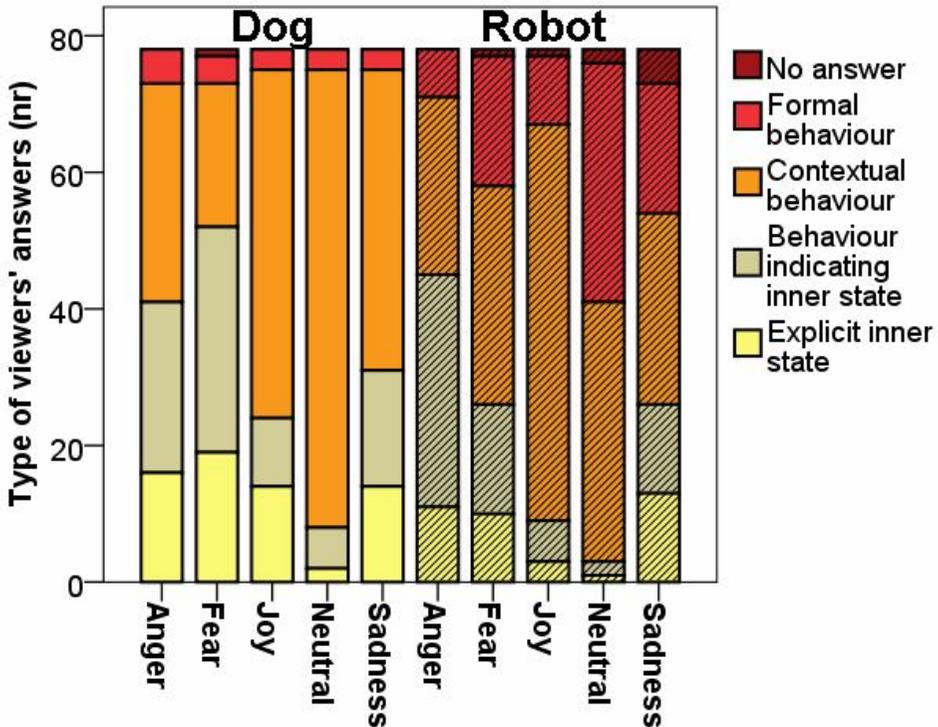
Using the above scoring system, we first compared subjects’ tendency to attribute an emotional state to the robot and the dog by averaging emotion scores of the 5-5 corresponding dog and robot video clips for each subject (paired-samples t-test). Then we tested if emotion scores for the emotionally loaded videos (average score for the videos of anger, fear, joy and sadness) differed from those of the neutral videos in case of both the dog and the robot (Wilcoxon tests). If subjects named an emotional state or a behaviour that indicates emotions (points 3 or 4), we also analysed whether their answer was correct or not, and compared it to the success rate in the multiple-choice questions (paired-samples t-test).

Multiple-choice questions. We first compared the rate of correct choices for each video clip to chance level (binomial test, test proportion 0.2). Next, the scores for the average success rate of the robot and dog videos were compared (paired-samples t-test). The effect of experience with dogs and order of presentation (dog first vs. robot first) was investigated using independent samples t-tests. Average certainty ratings for dog vs. robot videos were compared with paired samples t-test. The relation between certainty ratings and the proportion of correct responses was tested by Pearson correlation, while the difference in the certainty ratings of correctly vs. incorrectly assessed videos was compared by paired-samples t-test.

Results and Discussion

Open-ended questionnaire

Subjects readily attributed inner states to both the robot and the dog (Figure 20) and they did so more in case of the videos depicting emotions (mean emotion score for anger, fear, joy and sadness), than in case of the neutral video both in case of the dog ($Z=5.969$, $p<0.001$) and the robot ($Z=6.539$, $p<0.001$). However inner states were assigned more frequently to the dog than to the robot ($t_{(77)}=7.057$, $p<0.001$) videos. The order of presentation (robot videos first or dog videos first) did not have any effect on attributing emotions to neither the dog ($t_{(76)}=0.742$, $p=0.461$) nor the robot ($t_{(76)}=1.027$, $p=0.308$) videos.

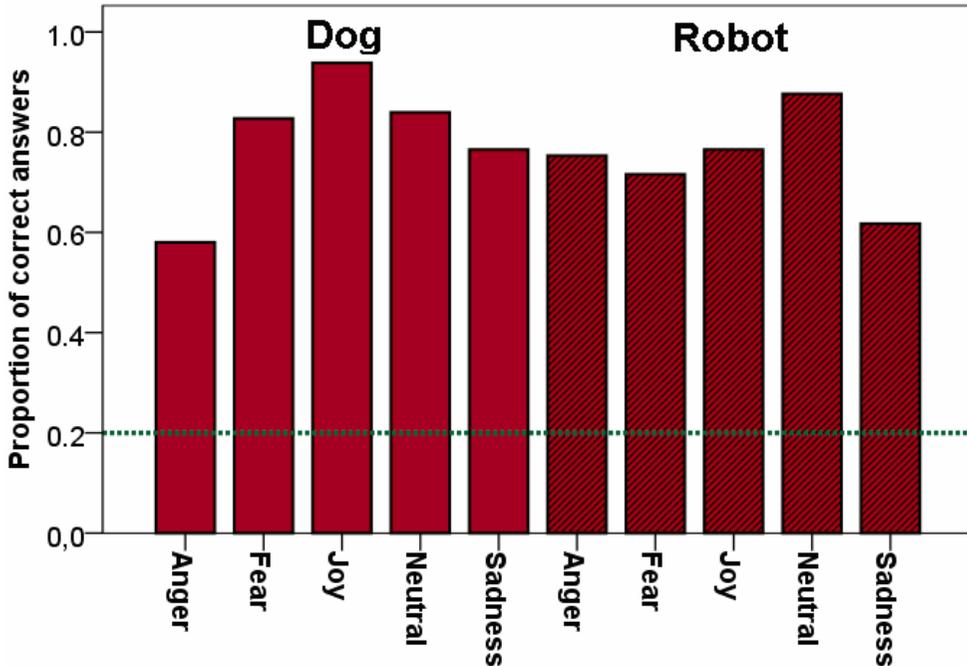


20. figure The distribution of the four categories shows how frequently the subjects characterized the videos by giving a formal behaviour description, naming a specific behaviour (Contextual behaviour), referring to a behaviour that indicates an inner state or naming a specific inner state explicitly (Explicit inner state).

Multiple-choice questionnaire

Subjects were considerably successful when they could choose from the 5 possible emotional states (Figure 21). They could identify all dog (all $p<0.001$; Binomial test, test proportion: 0.2), and all robot videos (all $p<0.001$) above chance level. We compared subjects' success regarding dog vs. robot videos and found that they were equally successful identifying dog and robot emotions ($t_{(80)}=1.512$, $p=0.135$). Subjects that had extensive experiences with dogs were not better at identifying inner states in case of either the dog ($t_{(72)}=1.254$, $p=0.214$) or the robot ($t_{(72)}=0.662$, $p=0.510$) videos. However subjects that saw the dog videos first were better at identifying the robot videos afterwards ($t_{(76)}=3.071$, $p=0.003$), while there was no such effect for the dog videos ($t_{(76)}=0.049$, $p=0.961$). Analysing data only for subjects that saw the robot videos first we also found that they could identify all dog (all $p<0.001$), and all robot (all $p<0.001$) videos above chance level. However in this subset subjects were more successful

identifying dog videos, than robot videos ($t_{(37)}=2.461$, $p=0.019$), although this difference did not remain significant after false discovery rate correction (Benjamini et al. 2001).



21. figure Proportion of correct answers in the multiple choice part of the questionnaire. Dotted line indicates chance level

In addition to the above dog-robot differences subjects also gave higher certainty ratings for the dog, compared to the robot videos ($t_{(80)}=4.601$, $p<0.001$). The overall certainty ratings of the subjects were not related to the percent of correct responses ($r=0.112$, $p=0.318$; Pearson correlations), but within individual subjects the correctly identified videos received higher certainty ratings, than the incorrect videos ($t_{(69)}=4.546$, $p<0.001$).

Results from the open-ended vs. multiple choice parts of the questionnaire

We also compared the rate of the correct answers for the open-ended questions (in those cases when subjects characterized the videos with an inner state or with a behaviour indicating an inner state: scores 3 or 4) with the rate of the correct answers in the multiple-choice part of the questionnaire. We found that subjects could identify the correct emotional/mental state equally well for both the dog ($t_{(67)}=0.271$, $p=0.787$) and the robot ($t_{(56)}=1.129$, $p=0.264$) videos. This suggests that subjects' first experience (1st viewing) did not modify too much their subsequent evaluation of the video clips (2nd viewing).

In the present study we suggested considering the human-robot social interaction as an inter-specific interaction, because when developing social robots for different functions it is not necessary and not even practical to use a human-like robot with a face or verbal abilities. First we showed that after viewing video clips about the robot that seemed to interact with them subjects attributed emotional states to the agent. Even though subjects were not told explicitly that we were interested in emotions and the questions were phrased neutrally, in a considerable proportion of the cases subjects interpreted the actions of the robot by crediting different – mainly correct – emotional/mental states to it. In addition, the lack of social contextual cues ensured that humans were restricted to the displays shown by the agents (robots and dogs).

In agreement with what could be expected subjects attributed inner states more often to a real dog than to a robot. We should not forget that from the viewpoint of robot development, subjects' (later users') impressions by definition cannot be false, because their subjective evaluation of the robot's expressive behaviours would validate the success of the social interactions of the robot. Therefore only these impressions can serve as evidence to support a method aiming at improving social behaviour of robots. Therefore, both the attribution of no inner states and the attribution of "incorrect" inner states means that the actions of the robot have not been properly set. Naturally, we cannot expect perfect recognition of emotional/inner states in robot-human encounters as there is no 100% success rate even in the case of human facial expressions (Elfenbein & Ambady 2002). Conversely, the embodiment and behavioural capacities of the robot will limit the subjects' possibilities of attributing inner states to it. These constraints and the lack of environmental cues constrained also the success rates in the present experiment.

So far the evaluation of expressive behaviours of social robots has been performed mainly by testing the recognition of the robots' human-like facial expressions in user studies. For example, the recognition rates of the six "basic" emotions were compared in case of robots which have the potential to be used in robot assisted therapy (Saldien et al. 2010). In these studies a multiple-choice questionnaire form was applied for the categorisation of emotions and the facial expressions of the robots were presented via photos or short video clips. The overall emotion recognition rate of the different robot faces was as follows: Kismet - 73% (Breazeal 2002), Eddie - 57% (Sosnowski et al. 2006), and Felix - 45% (Cañamero & Fredslund 2000), which are comparable to our result (58%). Furthermore our results fall in the range of recognition rates (50-83%) reported for human facial expressions (Elfenbein & Ambady 2002), and postures or body movements (de Gelder 2009).

The high rate of emotion recognition is not surprising, as in nature bodily and facial expressions are mostly used together and they provide redundant inner state information. We should note, however, that while facial gestures are more human specific, body movements are based on more general mammalian homologues (Plutchik 2001).

A potential advantage of the proposed dog model is underlined by the fact that experience with dogs did not help to evaluate the inner states presented on the videos. Similar results were reported by Tami & Gallagher (2009) who found that observers of video clips did not differ in their ability to properly label dog expressive behaviour according to their experiences with dogs, and subjects in general tended to give "holistic" descriptions of dog behaviour, such as "*the dog feels...*". Regarding dog vocal signals (barking), visual experience did not play a major role in the emotion attribution of congenitally blind individuals, blind individuals with previous visual experience, and sighted individuals (Molnár et al. 2010).

In sum, the results of the present study supported our hypothesis that the dog is a promising animal model for integrating function and sociality to develop more "companion-like" social robots for different purposes. We argued that human emotions and expressive behaviours can be too complex or ambiguous to implement in simple social robots. The recognition of simple expressive behaviours can be facilitated if they are based on lower level but more general biological primitives. This way we can adjust the relevant behaviour elements to the capacities

of a given robot to reach optimal expressive behaviours, without the need of adding extensive and complicated new features to the robot, which this way could fit primarily to its function.

Our results may facilitate the emergence of a new generation of robots which are equipped with ethologically more adequate behaviours, analogous to those displayed by dogs for affective communication. Importantly, we do not advocate to build robots that mimic a dog, as such attempts would constrain the behavioural repertoire and may lead to discomfort in some users (see Jones et al. 2008b). This study presented only one example for the proposed methodology. Admittedly, to support this broader hypothesis, further experiments need to be performed on different embodiments and inner states, with and without social contexts, and most importantly, observing live interactions between robots and humans instead of applying indirect encounters with a projected robot.

General Discussion

The above studies have presented how different comparative approaches to the study of social behaviour, as well as studies at different mechanistic levels can be used to answer the broad questions *what?* and *how?* of human social cognition. Studying the behaviour of phylogenetically distant (e.g. reptile) species can help us understand what are the basic and ancient mechanisms of sociality. The study of social behaviour in phylogenetically closely related species (primates) and how their behaviour resembles or differs from human social behaviour can unravel uniquely human social skills. Domestic species can be used to study how the special needs of adapting to the human environment have shaped social cognition in these species (compared to their wild relatives). The biological mechanisms underlying these social behaviours can also be studied in different ways. The candidate gene approach identifies genes (more specifically genetic polymorphisms) that contribute to the regulation of certain behaviours using a correlative method. On the other hand, by (intranasally) administering neuropeptides (e.g. oxytocin) we can observe the effect of this direct manipulation on certain behaviours.

Apart from the importance of these comparative frameworks for the understanding of human evolution there is also much applied and clinical relevance to all of these approaches. One example was presented from the field of social robotics, showing that by identifying the basic behavioural elements of emotional expressions, interactions with robotic agents that coexist with us could be made easier. This is in line with previous research suggesting the use of assistance dogs as a model of social robots (Koay et al. 2013; Gácsi et al. 2013a), and complements the long-held notion that domestic dogs are ideal models of human social disorders (Overall 2000). Research into the genetic and neurohormonal mechanisms underlying certain social skills also has a direct connection to the clinical field, as several human psychiatric disorders are characterised by social cognition deficits such as autism (Baron-Cohen et al. 2001), schizophrenia (Loughland et al. 2002) or fragile X syndrome (Garrett et al. 2004). The oxytocin system, that was also studied in the present thesis, has long been a target of pre-clinical investigations and recent research suggests that oxytocin administration can indeed be an effective treatment for social disorders (Heinrichs & Gaab 2007; Hollander et al. 2007); although see Bartz et al. (2011) for contradictory findings. As also discussed in Part IV, our results on the involvement of the oxytocin system in the regulation of social behaviour in dogs can aid research on human social deficits. Ultimately, each of the above presented comparative approaches – including the study of phylogenetically distant as well as closely related species – helps us understand human social behaviour and/or the underlying biological mechanisms, thus also might help understand its deficits and this way indirectly contribute to their treatment.

The present thesis has used the above comparative approaches to answer separate questions about social cognition. This is in a way an inherent property of the different frameworks as they are useful for different questions, however a combination of (at least some of) them could also lead to interesting new directions. The most straightforward way of doing this would perhaps be the combination of one comparative and one mechanistic approach. For example research into the oxytocin system presented in Part IV could nicely complement the study of primate

social behaviour (Part II). There have already been some attempts of doing this, and there is now evidence both from laboratory experiments (Snowdon et al. 2010) and field observations (Crockford et al. 2013) that oxytocin is involved in the regulation social affiliative behaviour in primates (tamarins *Saguinus oedipus* and chimpanzee *Pan troglodytes* respectively) as well. These examples nicely illustrate that with cleverly designed research setups we can at the same time gain information about both social behaviour and underlying mechanisms in a comparative framework. However this very advantage is also the danger of such studies, as the comparison is made between systems that differ not only in one but two aspects. In other words these studies – implicitly or explicitly – compare human social behaviour to primate social behaviour and the human oxytocin system to that of another primate species. Human social behaviour has long been known to differ from that of other primate species in many key aspects (e.g. Herrmann et al. 2007) and recent evidence has also demonstrated that for example some New World monkey species (specifically the squirrel monkey, *Simia sciureus*; the owl monkey, *Aotus nancymaae*; the capuchin monkey, *Cebus apella*; and the common marmoset, *Callithrix jacchus*) have a [P8] version of the hormone oxytocin, which differs from the human oxytocin in a single amino acid at position 8 that is substituted from leucine to prolin (Lee et al. 2011). It is not yet known how different forms of oxytocin affect for example binding to the oxytocin receptor or other cellular mechanisms, but the fact that the [P8] oxytocin is different from the human version of the hormone might affect the interpretation of studies on the effect of oxytocin in New World monkeys (and thus probably in non-human primates in general). Nevertheless if we bear in mind these possible confounds, than the oxytocin system is a good candidate for comparative research on the biological mechanisms of social behaviour, as it is a highly conserved neuropeptide and its evolutionary homologues are responsible for the regulation of social behaviour throughout the animal kingdom (Donaldson & Young 2008). The combination of a comparative and a mechanistic approach would thus be possible even in case of phylogenetically distant species (Part I), as for example vasotocin (a reptile homologue of the vasopressine–oxytocin hormones) has also been linked to certain social behaviours in reptiles (Goodson & Bass 2001) such as courting sounds, sexual behaviour, and birthing (Macdonald & Macdonald 2010). Future studies in this direction will obviously need to bear in mind that both the social behaviours and the biological mechanisms investigated can only remotely be related to their human analogues; nevertheless this approach could be crucial for investigating such theoretical claims that the neurohormone oxytocin had a key role during human evolution (Carter 2014). It is plausible to assume that complex social skills that newly emerged during hominization were – at least partly – built on already existing biological-neural systems (such as it has been shown to be the case for example with the cognitive skills of reading and arithmetic – Dehaene & Cohen 2007). If this is indeed the case, then identification of both social skills and regulating mechanisms that are evolutionarily ancient might bring us closer to unravelling such evolutionary processes.

Different comparative approaches could be (and indeed have already been) combined as well. In order to identify uniquely human social skills, shaped by the human environment the study of primates (Part II) and domestic species (Part III) in the same paradigm might be the most useful. For example studies on pointing following (e.g. Bräuer et al. 2006) received much attention because with this simple paradigm it was nicely shown that (*i*) the capacity is in some

way unique to humans; that means it is not present in non-human primates, and at the same time research on dogs (*Canis familiaris*) and wolves (*C. lupus*) has provided evidence that (ii) adaptation to the human environment has contributed to the emergence of this skill. In the present thesis the effect of communicative cues on object search performance in the “A-not-B” task was examined in both a primate (Part II) and a domestic (Part III) species, however based on data from solely two species the claims about human uniqueness and environmental adaptation remain purely speculative. This is also the most probable the reason why relatively few social skills have been put into this “meta-comparative” framework so far; in order to make such strong claims, that (i) a capacity is unique to humans (not present in other primates), many different primate species need to be examined; and in order to say that (ii) adaptation to the human environment has shaped a skill, members of both a domestic species and its phylogenetically closest wild relative need to be studied. A further difficulty in combining different comparative approaches and thus conducting studies that involve many different species is the standardization and ecological validity of the methods. The topic has been exhaustively covered in previous papers (see e.g. Mulcahy & Hedge (2012) for a meta-analysis on primate and dog pointing following methodology) with the main problem being that even the simplest tests cannot be properly standardized across species for a number of reasons: for example species differ in size, thus the distances in any experimental setup if kept the same then would differ in relative measures, the effect of which is unknown and hard to quantify; keeping conditions and thus testing environments also differ considerably across species causing additional unwanted variation in the data; and perhaps even more importantly the degree to which a certain experimental problem is part of the natural environment of a species cannot be controlled either. Despite these constraints, the long known system theory principle stands: the combination of different comparative approaches can always tell us something more, or at least different, than the sum of the separate approaches, thus however difficult efforts should be made in this direction. Apart from this – simply put – “phylogeny versus adaptation” framework another possible combination of comparative approaches could take advantage of the fact that identifying basic elements of social behaviour is the goal of both the study of phylogenetically distant species (Part I) and social robotics (Part V), as both of them are aiming at studying social functions in very limited – natural or artificial – “embodiments”. The combination of these two approaches – especially in case of social behaviours that are relatively wide-spread, so to say “universal”, across the animal kingdom – might also be fruitful, and indeed some recent research is being carried out with the robotic counterparts of relatively simple organisms (Halloy et al. 2007).

The combination of approaches at different mechanistical levels (Part IV) can also help understand the complex picture. We have seen for example that polymorphisms in the oxytocin receptor gene influence certain aspects of social behaviour, and the effects of intranasal oxytocin administration have also been shown in a different setup. These two effects, however, are most probably not independent from each other, as it is plausible to assume that individuals with different receptor genotypes would react differently (or to a different extent) to neurohormone administration. Obviously apart from these two approaches presented in this thesis there is an almost infinite number of additional approaches that we might consider for a combined mechanistical framework. Our options are considerably different according to the

species under investigation – as the majority of techniques have been developed and/or validated for certain species only –, but for example in the case of domestic dogs (that was the species used in Part IV of the present thesis) there are several additional measures that one might consider. Peripheral measures of certain hormones (including oxytocin) have for example been related to certain behaviours and/or behavioural pretreatments (Odendaal 2003; Rehn et al. 2014), and thus might provide some useful information about background mechanisms following neurohormone administration. Neurohormonal measures might be nicely complemented by physiological data such as heart rate (Gácsi et al. 2013b) and by the measurement of neural activity for example by EEG (Törnqvist et al. 2013; Kis et al. 2014), or fMRI (Tóth et al. 2009; Berns et al. 2013; Andics et al. 2014). These latter techniques are currently in the phase of methodological development, thus their use in the above mentioned integrative framework most probably would not be without problems, but the complexity of the system under investigation will ultimately require the use of multiple-level approaches.

In sum we have seen how different approaches can be used to answer different sub-questions in the field of comparative social cognition, and the possibility of combining these approaches in an integrative framework has been discussed. All these data presented in this thesis and that future research will collect can thus hopefully bring us closer to understand the perhaps most complex phenomena one can ever study: human social cognition.

Appendices

Appendix 1

Validation of a dog social behaviour test for phenotyping purposes⁹

Background

Although the dog has been proved to be an ideal behavioural genetic model species (Parker & Ostrander 2005), gene \times behaviour association studies using individual phenotyping are scarce. The most widely used method relies on breed stereotypes provided by experts such as dog-trainers (Jones et al. 2008b; Chase et al. 2009). In the first part of this study our aim was to develop in a group of pet German Shepherd dogs a test series measuring human-directed social behaviour. We intended to find behavioural scales with high internal consistency and inter-observer reliability that is crucial for measuring behavioural traits (Diederich & Giffroy 2006). In order to further validate the behavioural scales, in the second part of the study we applied the same test on Border Collies of two different countries in order to see whether the same behavioural scales are applicable.

Method

Subjects were 104 privately owned adult (>1 year; mean age \pm SD: 3.88 \pm 2.55) German Shepherd dogs (males: 58, females: 46). None of the subjects were closely related, i.e. littermate and parent-offspring relationships were excluded. In order to describe and validate a test series measuring human-directed social behaviour subjects participated in a standard test series conducted outdoors, comprised of the following episodes:

1. Greeting (adapted from Netto & Planta 1997): the owner (O) stands motionless next to the dog and holds the leash. An unfamiliar experimenter (E) approaches them in a friendly way. E stops out of reach of the leash and waits for 3 seconds. If the dog is not aggressive, E steps next to the dog then pets the dog's head and back. Then E steps away and waits for another 3 seconds.

2. Separation from the owner (adapted from Topál et al. 1998): the dog is tethered to a tree on a leash, while O is hiding behind an object (e.g. a big tree) which is at 5-6 m from the dog, and blocks the dog from seeing the owner. After 1 min has elapsed E approaches the dog and greets it (see description at Test 1: Greeting). Then E initiates play with a tug for 30 seconds. Then E steps back to the camera. After 1 minute has elapsed, E asks the O to come back and greet the dog (see description at Test 1: Greeting). Afterwards O initiates play with a tug.

3. Problem solving (adapted from Passalacqua et al. 2011): E puts a piece of food into a small cage that can be retrieved by rolling over the cage. The O stands 1 m in front of the cage, holds the leash of the dog and is not allowed to speak or gesticulate. The dog has 1 minute to manipulate the cage. The trial ends when the dog gets the food, or after the 1 minute elapsed (in which case the E gives the food to the dog). This trial is repeated once.

4. Threatening stranger (adapted from Vas et al. 2005): O stands motionless next to the dog and holds the leash. E steps back 10 meters, and approaches the dog slowly, by leaning forward her upper body and staring at the eyes of the dog. E stops approaching when the dog

⁹ This chapter is based on: **Kis, A., Bence, M., Lakatos, G., Pergel, E., Turcsán, B., Pluijmakers, J., Vas, J., Elek, Z., Brúder, I., Földi, L., Sasvári-Székely, M., Miklósi, Á., Rónai, Z., Kubinyi, E.** (2014). Oxytocin receptor gene polymorphisms are associated with human directed social behavior in dogs (*Canis familiaris*). *PLoS ONE*, 9(1) e83993

shows signs of aggression, severe fear or when she reached the dog. Finally, the E steps back to the starting point, crouches, and asks the O to let the dog free. Then she starts to call the dog in a friendly way.

5. Hiding (adapted from Kubinyi et al. 2012): E takes the dog on the leash, meanwhile the O is asked to hide behind a large tree 15-20 m away from the dog. After 30 seconds, independently from the orientation of the dog, the E releases the dog and says "Go!". If the dog does not start to move immediately, the E once pushes it gently by touching the rear end of the dog. If the dog does not start to move within 5 seconds then the E asks the owner to call the dog.

Episode	Variable (Abbreviation)	Definition 0-3 score			
<i>Greeting</i>	Latency of approaching E (GrApp)	0 s	1-5 s	5-15 s	Does not approach
	Latency of following E (GrFoll)	0 s	1-5 s	5-15 s	Does not follow
<i>Separation</i>	Duration of orientation to O (1) (SepOriO1)	0 %	1-50 %	51-99 %	100 %
	Latency of approaching E (SepAppE)	0 s	1-5 s	5-15 s	Does not approach
	Latency of following E (SepFollE)	0 s	1-5 s	5-15 s	Does not follow
	Duration of orientation to O (2) (SepOriO2)	0 %	1-50 %	51-99 %	100 %
	Latency of approaching O (SepAppO)	0 s	1-5 s	5-15 s	Does not approach
	Latency of following O (SepFollO)	0 s	1-5 s	5-15 s	Does not follow
	Duration of playing with the O (SepPlayO)	0%	1-50%	51-99%	100%
<i>Problem solving</i>	Number of orientations to O (1) (ProblOriO1)	0 %	1-50 %	51-99 %	100 %
	Number of orientations to E (1) (ProblOriE1)	0 %	1-50 %	51-99 %	100 %
	Number of orientations to O (2) (ProblOriO2)	0 %	1-50 %	51-99 %	100 %
	Number of orientations to E (2) (ProblOriE2)	0 %	1-50 %	51-99 %	100 %
	Jumping ups (ThreJump)	0	1	2	≥3
<i>Threatening approach</i>	Friendly–Aggressive (subjective score) (ThreFrieAgg)	Aggressive	Neutral	2	Friendly
	Latency of approaching during calling (ThreCall)	0 s	<10 sec	10-30 sec	Does not approach
<i>Hiding</i>	Latency of approaching O (HideAppO)	0 s	1-5 s	5-15 s	Does not approach

4. table Behavioural variables coded in each test. Definitions for the 0-3 scores of each behavioural variable coded during the five tests are provided.

Behavioural variables were coded on a 0-3 scale in each episode (Table 4). The video protocol can be found at: <http://www.cmdbase.org/web/guest/play/-/videoplayer/222>

Then we applied the same test series to N=103 adult (>1 year; mean age \pm SD: 4.28 \pm 2.74) Border Collies (males: 46, females: 57) from two countries (59 from Hungary and 44 from Belgium) in order to test if the test series is valid for a different breed and for different countries.

Statistical analysis

First, a Principal Component Analysis was carried out on all behavioural variables coded for German Shepherds and behavioural scales were created. Internal consistency of the scales was characterized by Cronbach's Alpha values. In order to check inter-rater reliability 20 test videos were coded by two independent raters and interclass correlation (Lessells & Boag 1987) was calculated between them for each of the four behavioural scales.

Second, behaviour of all subjects was characterized by calculating the behavioural scales based on the structure obtained in German Shepherd dogs, and the two populations of Border Collies as well as the two different breeds were compared (independent samples t-tests).

Results

The Principal Component Analysis of German Shepherd dog behavioural data resulted in four behavioural scales (Table 5):

	Proximity seeking	Reaction to separation from owner	Friendliness	Looking at humans
SepAppE	0.812			
SepFolle	0.766			
GrApp	0.511			
SepPlayO	0.447			
ThreCall	0.445			
SepFollo	0.424			
SepOriO2		0.880		
SepOriO1		0.857		
HideAppO	0.237	0.643		0.207
ProblOriE2			0.884	
ThreFrieAgg			0.795	
ThreJump			0.550	
ProblOriO2				0.829
ProblOriO1				0.777
ProblOriE1		0.207		0.557

5. table Factor loads of the different variables on each behavioural scale. Behavioural variables that were related to any of the four scales according to the Principal Component Analysis and their factor loads are shown; values <0.2 are suppressed for the sake of clarity

Proximity seeking is related to how willingly the dog approaches and interacts with both the owner and a stranger and is composed of the following variables: *Greeting Approach E*; *Separation Approach E*, *Follow E*, *Follow O*, *Play with O*; *Threatening approach Call* (Cronbach α =0.628).

Reaction to separation from owner is related to how intensely the dog shows owner-directed behaviours when left alone or with a stranger and is composed of the following variables: *Separation Orientation to O (1)*, *Orientation to O (2)*; *Hiding Approach O* (Cronbach $\alpha=0.753$).

Friendliness is related to the dog's behaviour in reaction to a threatening stranger and to a passive stranger while facing a problem box and is composed of the following variables: *Problem solving Orientation to E (2)*; *Threatening approach Friendly–Aggressive*, *Jumping ups* (Cronbach $\alpha=0.525$).

Looking at humans is related to the number of times the dog looks at the passive owner and stranger while facing a problem box and is composed of the following variables: *Problem solving Orientation to O (1)*, *Orientation to O (2)*, *Orientation to E (1)* (Cronbach $\alpha=0.611$).

According to the interclass correlations, all four scales are highly reliable between raters: Proximity seeking: $r = 0.961$, $p < 0.001$; Reaction to separation from owner: $r = 0.806$, $p < 0.001$; Friendliness: $r = 0.861$, $p < 0.001$; Looking at humans: $r = 0.943$, $p < 0.001$.

Internal consistency of the behavioural scales was also high for Border Collies: Proximity seeking: $\alpha=0.692$; Reaction to separation from owner: $\alpha=0.502$; Friendliness: $\alpha=0.695$; Looking at humans: $\alpha=0.739$, thus validating the behavioural scales on an independent sample.

Behaviour of Border Collies from the two countries did not differ with respect to Proximity seeking ($t_{(101)}=1.758$, $p=0.082$), Reaction to separation from owner ($t_{(101)}=0.528$, $p=0.598$) and Friendliness ($t_{(101)}=0.354$, $p=0.724$), although Belgian dogs scored higher for Looking at humans ($t_{(101)}=3.597$, $p=0.001$).

Behaviour of German Shepherds and Border Collies on the other hand was considerably different with Border Collies showing more Proximity seeking ($t_{(213)}=3.240$, $p=0.001$), a weaker Reaction to separation from owner ($t_{(213)}=6.493$, $p < 0.001$), less Friendliness ($t_{(213)}=2.561$, $p=0.011$) and more Looking at humans ($t_{(213)}=2.540$, $p=0.012$).

Appendix 2

Identification of canine OXTR polymorphisms¹⁰

Background

Polymorphisms in the OXTR gene have been implicated in the regulation of a wide range of human social behaviours (Gillath et al. 2008; Rodrigues et al. 2009; Chen et al. 2011). Furthermore it has already been shown that the similarity between the human and the dog OXTR gene is high (Marx et al. 2011). However no information is yet available on the dog OXTR gene polymorphisms. Thus the aim of this study was to identify SNPs in the OXTR gene of German Shepherds and Border Collies, as well as to characterize these two breeds for allele frequencies, Hardy-Weinberg equilibrium and Linkage Disequilibrium.

Method

Sequencing. Buccal samples were collected from all dogs participating in the validation of the above social behaviour test in a non-invasive way, with cotton swabs from the inner surface of the cheek. Genomic DNA was extracted from buccal swabs using standard protocol. The sequence of the dog OXTR gene was obtained from the GenBank (<http://www.ncbi.nlm.nih.gov/>) and Ensembl (<http://www.ensembl.org/>) databases, accession numbers were as follows: NC_006602 and ENSCAFG00000005553 in the two databases, respectively. The sequence of protein coding and the surrounding regulatory regions (582 bp of 5' flanking region and 585 bp of 3' flanking region) of dog OXTR gene was determined by polymerase chain reaction (PCR) amplification and subsequent direct sequencing performed on 3-3 individuals of five different dog breeds (German Shepherd, Siberian Husky, Beagle, Border Collie, Golden Retriever), respectively. PCR primers were designed by NCBI/Primer-Blast (<http://www.ncbi.nlm.nih.gov/tools/primer-blast/>).

	Primer	Sequence (5'-3')	T _A (°C)
5' flanking region	Forward	GGATGGTGCTGAGCGGGGA	62
	Reverse	GGCCGTGCGGTTGCCCT	62
exon 1 5' region	Forward	GTGAGCGCTCGGTCTTCTC	56
	Reverse	CAGCGGCTGGCAGATGG	56
exon 1 3' region	Forward	CATGTTGCCTCCACCTACC	56
	Reverse	GCCCCGCTCGCTACCTT	56
exon 2	Forward	GAAAGGCCATTCTCAGGAAA	52
	Reverse	CCCCCATCATCTTCTACCA	52
3' flanking region	Forward	TAGACAGTCCGCCCTTGGTGG	58
	Reverse	CACCTTCTGACATGCTGGTGGCC	58

6. table Sequencing primers and annealing temperatures used for PCR amplification of dog OXTR gene regions

The Qiagen Hot-StarTaq polymerase kit was used for PCR amplification. The reaction mixture contained 1 μ M of each primer (Table 6), approximately 5 ng of DNA template, 200 μ M dNTP, 0.025 U HotStarTaq DNA polymerase, 1x buffer, and 1x Q-solution supplied

¹⁰ This chapter is based on: **Kis, A., Bence, M., Lakatos, G., Pergel, E., Turcsán, B., Pluijmakers, J., Vas, J., Elek, Z., Brúder, I., Földi, L., Sasvári-Székely, M., Miklósi, Á., Rónai, Z., Kubinyi, E.** (2014). Oxytocin receptor gene polymorphisms are associated with human directed social behavior in dogs (*Canis familiaris*). *PLoS ONE*, 9(1) e83993

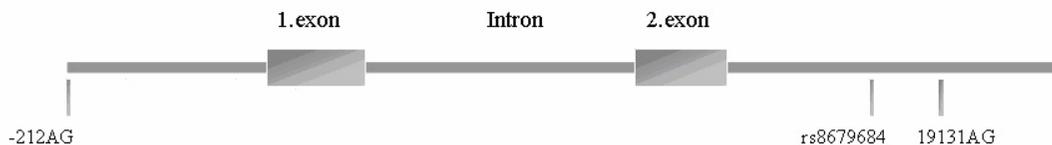
together with the enzyme. The PCR cycle consisted of an initial denaturation at 95 °C for 15 minutes, 35 cycles of 1-min denaturation at 95 °C, 1-min annealing at various temperatures (Table 6), a 1-min extension at 72 °C, and a 10-min final extension at 72 °C. The PCR reaction was performed in a total volume of 30 µl. The obtained PCR products were cleaned by Wizard SV Gel and PCR Clean-Up System (Promega, A9282) and sequenced in both forward and reverse directions with the same PCR primers (Macrogen Europe). SNPs were identified by aligning and comparing the sequence data with an Internet program (<http://www.genome.jp/tools/chustalw/>).

Genotyping. From the three polymorphisms identified (see Results below) –212AG SNP was genotyped by PCR-RFLP method. PCR amplification was performed as described above using 5'-CCA TTG GAA TCC GCC CCC T-3' forward and 5'-CAC CAC CAG GTC GGC TAT G-3' reverse primers. Annealing temperature was 56 °C and total reaction volume was 10 µl. PCR products were incubated for 3 h at 37 °C in a restriction enzyme mixture containing 0.5 U/µl Hpy99I restriction enzyme (NEB), 1x BSA and 1x NEB4 buffer. Total reaction volume was 16 µl. The digested PCR products were analyzed by conventional submarine agarose gel electrophoresis (Biocenter, Szeged, Hungary), using 2.5% agarose gel and visualized by ethidium bromide staining.

19131AG and rs8679684 SNPs were genotyped by real-time PCR using sequence specific TaqMan probes with minor groove binding (MGB) quencher. Primers were designed by Primer Express 3.0: rs8679684: forward primer: 5'-CTC CTT TAT TTT GGG ATC TTG TGA A-3', reverse primer: 5'-CCT GCT CCT TAT TCT GAG CTT AGA A-3', probe specific for T allele: 5'-FAM-AGT GGT AAG TAT AGG ATT G-MGB-3', probe specific for A allele: 5'-VIC-AGT GGT AAG TAA AGG AT-MGB-3'. Primers and probes for 19131AG SNP: forward primer: 5'-AGC AGG AAT GGG ACC TCA GAT-3', reverse primer: 5'-GCA AAA GTA AAA GCA CTC TGA AGT CA-3', probe for G allele: 5'-VIC-TGGTGCTAATGTCCT-MGB-3' and for A allele: 5'-FAM-TGG TGC TAA TAT CCT-MGB-3'. Fluorescent signals were detected both real-time and after the PCR amplification, and were evaluated by the Sequence Detection Software 1.4. Allele frequencies were calculated for both breeds (and for the Hungarian and Belgian populations of Border Collies) separately. Hardy-Weinberg Equilibrium and Linkage Disequilibrium analyses were also carried out for the two breeds separately by Haploview 4.2 program (Barrett et al. 2005).

Results

By direct sequencing of protein coding and the surrounding regulatory untranslated regions of the dog OXTR gene one known (rs8679684) and two novel (–212AG, 19131AG) single nucleotide polymorphisms (SNP) were found. The –212AG SNP is located in the 5' flanking region, whereas rs8679684 and 19131AG SNPs can be found in the 3' untranslated region of the gene (Figure 22). The identified polymorphisms were subsequently genotyped in 104 German Shepherds and 103 Border Collies used for the validation of the behavioural test. Linkage analysis revealed that the rs8679684 and 19131AG SNPs are in strong linkage disequilibrium both in German Shepherds ($D' = 0.98$, $R^2 = 0.96$) and in Border Collies ($D' = 1.0$, $R^2 = 1.0$).



22. figure The three polymorphisms identified in the dog OXTR gene. The figure shows the canine OXTR gene with exons 1 & 2, the intron and the surrounding regulatory regions. Polymorphisms in the 5' and 3' UTR regions are marked with their rs number if applicable or with their position and base change.

Allele frequencies of the two breeds are presented in Table 7. Hungarian and Belgian Border Collies did not differ in allele frequencies for any of the three investigated SNPs (19131AG: $\chi^2_{(2)}=5.181$, $p=0.075$, -212AG: $\chi^2_{(2)}=4.384$, $p=0.112$, and rs8679684: $\chi^2_{(2)}=4.121$, $p=0.127$). Both breeds were in Hardy-Weinberg equilibrium for all three polymorphisms (Table 7).

	-212AG				rs8679684				19131AG			
	AA	AG	GG	HWE	AA	AT	TT	HWE	AA	AG	GG	HWE
German Shepherd	0.12	0.48	0.39	$p=0.876$	0.38	0.47	0.15	$p=1.000$	0.37	0.49	0.14	$p=0.749$
Border Collie (Hungary)	0.10	0.31	0.47	$p=0.203$	0.00	0.03	0.92	$p=1.000$	0.00	0.03	0.97	$p=1.000$
Border Collie (Belgium)	0.02	0.23	0.66	$p=1.000$	0.02	0.11	0.80	$p=0.486$	0.02	0.14	0.84	$p=0.601$

7. table Allele frequencies for the two breeds studied. The proportion of each genotype is provided for German Shepherds and the two populations (Hungary, Belgium) of Border Collies separately. Statistical tests for Hardy-Weinberg Equilibrium (HWE) are also provided.

Appendix 3

*The effect of intranasal oxytocin on dog heart rate and heart rate variability*¹¹

Background

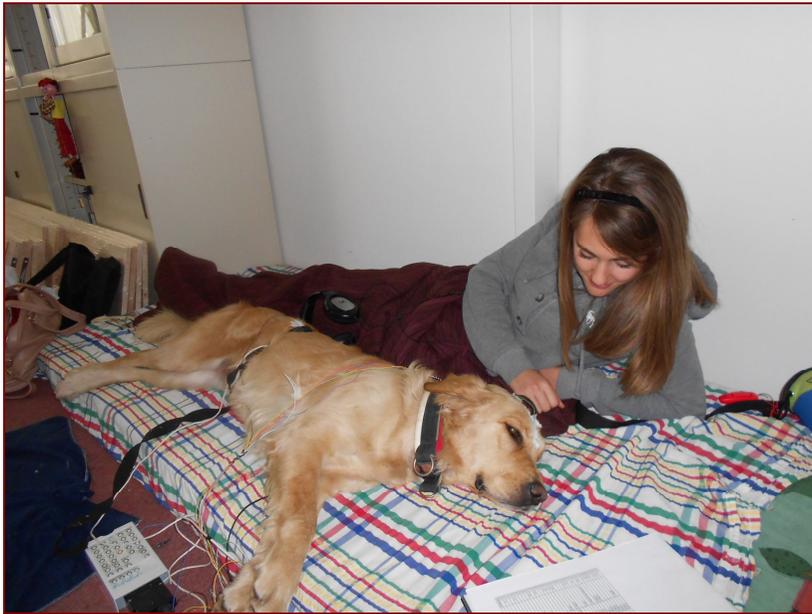
In recent years an increasing number of studies has used intranasal oxytocin administration in order to explore its effects on human social cognition (Heinrichs et al. 2009; Van IJzendoorn & Bakermans-Kranenburg 2012). There is a tacit assumption in the literature that intranasal administration of oxytocin enables direct access of the peptide to the central nervous system (CNS), thus providing a useful method for studying the specific effects of this neuropeptide on the regulation of behaviour. This is based on the work by Born et al. (2002) showing that after intranasal administration of melanocortin, vasopressin and insulin to human subjects the concentration of these peptides was elevated in the cerebrospinal fluid. More recently Neumann et al. (2013) provided more direct evidence for an association between intranasal administration of oxytocin and the increased level of this neuropeptide in both the hippocampus and amygdala.

In humans the effect of intranasal oxytocin on both the behavioural and physiological level are well documented. The increasing interest in dog social cognition (Morell 2009) makes it timely to study the effect of intranasal oxytocin in this species as well. In order to validate the intranasal administration of oxytocin in dogs we intended to show that it has parallel effects on a physiological parameter – heart rate and heart rate variability – as seen in humans (Light et al. 2005; Gutkowska & Jankowski 2008; Kemp et al. 2012; Kis et al. 2013).

Methods

Our subjects were N=10 pet dogs (3 males and 7 females with a mean age \pm SD of 4.33 \pm 2.69 years). All subjects participated in two test occasions receiving oxytocin and placebo nasal spray (in a counterbalanced order) followed by a 40-minutes waiting period and an ECG recording. The ECG recording took place in a room equipped as an ordinary office in the Department of Ethology, ELTE, Budapest that additionally had a mattress on the floor for the dog and its owner to sit on it (Figure 23). After a 5-10 minutes exploration and familiarization period the owner took place on the mattress and assisted the experimenter throughout the process of fixing two surface attached electrodes onto the dog's chest (second rib on both the left and right side). Gold-coated Ag|AgCl electrodes fixed with EC2 Grass Electrode Cream (Grass Technologies, USA) were used for the recordings. The electrode placement was followed by 4 minutes quiet resting (during which the dog was in a laying position), and then by a 1 minute long recording (during which the dog was still in a laying position). Signals were collected, prefiltered, amplified and digitized at a sampling rate of 249 Hz/channel by using the 30 channel Flat Style SLEEP La Mont Headbox with implemented second order filters at 0.5 Hz (high pass) and 70 Hz (low pass) as well as the HBX32-SLP 32 channel preamplifier (La Mont Medical Inc., USA). R peaks were manually detected, and RR intervals were measured using the Fercio program (© Ferenc Gombos 2012). Heart rate (HR; 1/min) was derived from RR interval averages (60/RR), and heart rate variability (HRV; sec) was calculated as the standard deviation of RR intervals (see e.g. Gácsi et al. 2013a for similar measures).

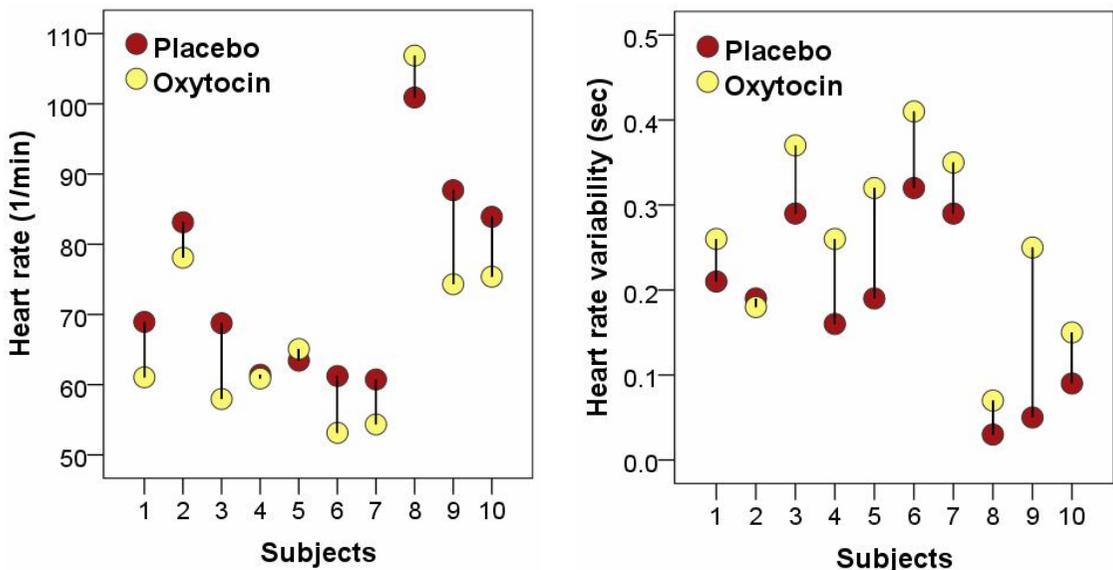
¹¹ This chapter is based on: **Kis, A., Hernádi, A., Gácsi, M., Topál, J. (under revision)**. Oxytocin induces an 'optimistic' cognitive bias in dogs (*Canis familiaris*). *Hormones and Behavior*



23. figure Photograph of the test setup used for the ECG recordings

Results and discussion

A considerable individual variation could be observed in the effect of oxytocin on HR and HRV (Figure 24). However at the group level oxytocin significantly decreased HR ($t_{(9)}=2.810$, $p=0.020$) and increased HRV ($t_{(9)}=4.472$, $p=0.002$).



24. figure The effect of oxytocin on heart rate and heart rate variability (measured as the standard deviation of the RR intervals) in ten individual dogs

These results parallel those of previous studies on humans (Light et al. 2005; Gutkowska & Jankowski 2008; Kemp et al. 2012; Kis et al. 2013) and thus indicate that intranasal administration of oxytocin might be a valid approach to study its effects on dog social cognition. Furthermore the individual variation in the effect of oxytocin on HR and HRV make it a good indicator of the physiological effect of oxytocin and might thus be used as a covariate in future behavioural studies.

Appendix 4

*Comparison of different Cognitive Bias procedures for testing dogs*¹²

Background

There is an increasing interest in measuring animal welfare (Boissy et al. 2007; Yeates & Main 2008) and a paradigm that is becoming widely accepted to determine affective state and animal welfare is the Cognitive Bias approach (Harding et al. 2004). This test starts with a discrimination learning phase when the subjects learn that one stimulus (sound, colour, location, etc.) is negative, while another one is positive. After having learned the task, animals typically show no response to the negative stimuli or they respond with a higher latency. In the test trial(s) the subjects' response to an ambivalent stimulus (that is between the negative and the positive stimuli; e.g. grey in case of black-white colour discrimination) is measured. In case of a positive affective state an "optimistic" response is expected for the ambivalent stimuli (Mendl et al. 2009), that is animals respond almost as if it was a positive stimuli (e.g. with low latency). This approach has been proved to be an effective testing tool in case of several animal species including rats (Burman et al. 2009), sheep (Doyle et al. 2010), pigs (Scollo et al. 2014) starlings (Bateson & Matheson 2007), and honeybees (Bateson et al. 2011).

In recent years dogs have become a widely studied species. This is most probably due to the intriguing fact that although dogs only possess relatively poor understanding of physical cognition (e.g. landmark learning: Milgram et al. 1999, invisible displacement in object permanence studies: Fiset & Leblanc 2007), they excel at socio-cognitive tasks (Hare & Tomasello 2005). Despite their apparent difficulties in discrimination learning tasks, the Cognitive Bias approach has been implemented (Mendl et al. 2010) and successfully used (Burman et al. 2011; Müller et al. 2012) in case of dogs as well.

Probably due to the huge amount of research on dog cognition being carried out (Morell 2009), it is a common problem that researchers intending to use the same study protocol end up with subtle differences in their methods, that might influence their results in unexpected and/or uncontrolled ways. The need for standardisation in dog behaviour research has already been raised in the field of temperament assessment (Taylor & Mills 2006), however it is still a common practice to carry out cognitive tests with slight modifications to previous methods. For example one experiment studying how canines follow human pointing gestures used a clicker reinforcement after correct choices together with the food reward (Udell et al. 2008) as opposed to other studies that did not (Hare et al. 2002; Virányi et al. 2008). Another similar case is that experiments studying the social aspects of the "A-not-B" error (a common object permanence task; see also Part III.) in dogs have been carried out without taking into consideration the end position of the experimenter after baiting (Topál et al. 2009b; Marshall-Pescini et al. 2010; Kis et al. 2012b). Variation also exists in the way the Cognitive Bias test has been performed, for example Müller et al. (2012) used a different training criteria than the original (Mendl et al. 2010) study.

As a first step in a long way that should lead us to unravel the impact of such subtle methodological differences on the conclusions we draw about dog cognition, we asked whether

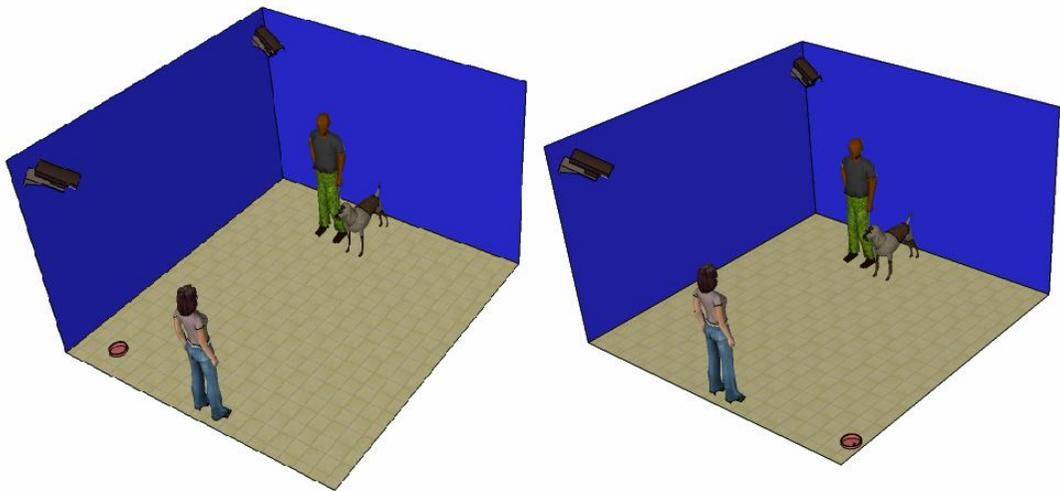
¹² This chapter is based on unpublished data by **Kis, A., Kanizsár, O., Sümegei, Z., Gaugg, A., Kovács, K., Virányi, Z., Gácsi, M., Topál, J.** with the provisional title of: Discrimination learning in dogs (*Canis familiaris*): Preconsiderations for applying the Cognitive Bias approach

the performance of dogs in a discrimination learning task was influenced by slight differences in the training protocol.

Study I.

Method

Our subjects were N=62 adult (>1 year old) pet dogs (mean age±SD: 2.7±1.4 years, 26 males). Subjects were divided into four groups (N=19, 17, 10, 16 respectively) participating in different types of discrimination training that all aimed at teaching the dog that if a food bowl was placed to one side of the room, then it always contained a food reward, whilst if placed to the opposite side, then it was always empty (see the Cognitive Bias procedure of Mendl et al. 2010 for details). In case of both training types (Figure 25) the dogs were held by their owners while a female experimenter, who was standing on the opposite side of the room, put a food bowl to one of two locations equidistant (3 meters) from the dog at the left or right side of the room (2 meters apart from each other). The dog was then released and allowed free access to the food bowl that either contained a food item (positive location) or was empty (negative location). Then the owner called the dog back and the next trial started. The experimenter recorded the dogs' latency to approach the food bowl in each trial. Training continued until dogs reached the following criteria: the latency for each of the last five negative trials was higher than any of the latencies for the last five positive trials (Mann Whitney test, $Z=2.694$, $p=0.008$).



25. figure Experimental arrangement

Apart from the general procedure the four training types differed in several minor issues, all of them being plausible procedural differences between dog cognition studies claiming to use the same methodology; such as identity of the experimenter, reward used, what the experimenter says, whether the owner is allowed to talk, order of trials, food bowl used, coding of choice, incorporating the task in a test series or applying it on its own. The 1st and 2nd training types were identical with the only difference that they were carried out by different experimenters, thus aiming to test if careful control of methodological details leads to identical results. The 3rd and 4th training types differed from the previous two in many aspects (Table 8), thus aiming to test if minor methodological differences can cause substantial differences in the results.

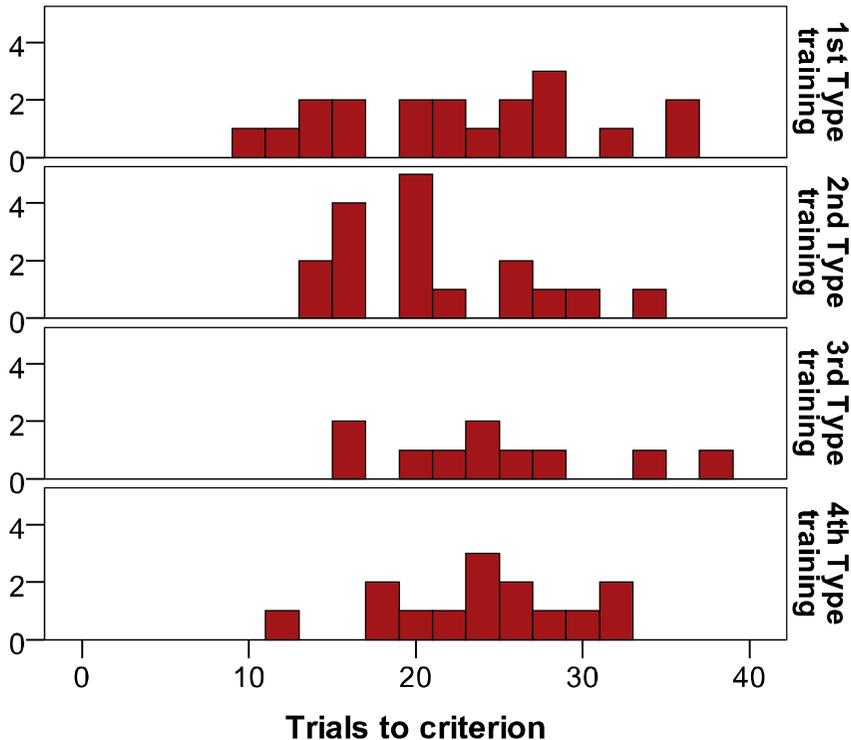
1st type training	2nd type training	3rd type training	4th type training
Carried out by Experimenter1 (AG) Sausage is used as reward Experimenter pronounces a happy / sad expression when the dog approaches the positive / negative food bowl	Carried out by Experimenter2 (OK) Sausage is used as reward Experimenter pronounces a happy / sad expression when the dog approaches the positive / negative food bowl	Carried out by Experimenter3 (ZsS) Dry food is used as reward Experimenter is silent after the dog approaches the food bowl	Carried out by Experimenter4 (AK) Dry food is used as reward Experimenter pronounces a happy / sad expression when the dog approaches the positive / negative food bowl
The owner is not allowed to talk to the dog at the beginning of the trials	The owner is not allowed to talk to the dog at the beginning of the trials	The owner is not allowed to talk to the dog at the beginning of the trials	The owner is allowed to give one command at the beginning of each trial to encourage the dog to search
The order of trials is fixed: PPNPNN – PPNPNN – etc. The food bowl is a pot washer, so that the dog potentially can already see from relatively further away if it is baited	The order of trials is fixed: PPNPNN – PPNPNN – etc. The food bowl is a pot washer, so that the dog potentially can already see from relatively further away if it is baited	The order of positive / negative trials is random The food bowl is a flowerpot, so that the dog cannot see if it is baited or empty until it goes close to it	The order of trials is fixed: PPNPNN – PPNPNN – etc. The food bowl is a pot washer, so that the dog potentially can already see from relatively further away if it is baited
The latency is measured until the dog touches the food bowl	The latency is measured until the dog touches the food bowl	The latency is measured until the dog touches the food bowl	The latency is measured until the dog crosses a line at a distance of 10 cm from the food bowl
Subjects participate in several other tasks before the Cognitive bias test	Subjects participate in several other tasks before the Cognitive bias test	Subjects only participate in the Cognitive Bias test	Subjects only participate in the Cognitive Bias test

8. table Differences in the procedures of the different training types

For all subjects, the experimenter noted the latency to reach the food bowl in each trial, and mean latencies for the last five positive and the last five negative trials were calculated. A paired samples t-test was carried out to confirm the difference between positive and negative trials. The four training types were compared with respect to these mean latencies, as well as the number of trials necessary to reach criterion (ANOVA).

Results

Dogs in all four training types successfully reached criterion after a comparable amount of trials (24.7 ± 7.1 , 20.41 ± 6.08 , 22.42 ± 7.63 and 23.9 ± 5.7 trials respectively; ANOVA $F_{(3, 58)} = 0.946$, $p = 0.425$; Figure 26).

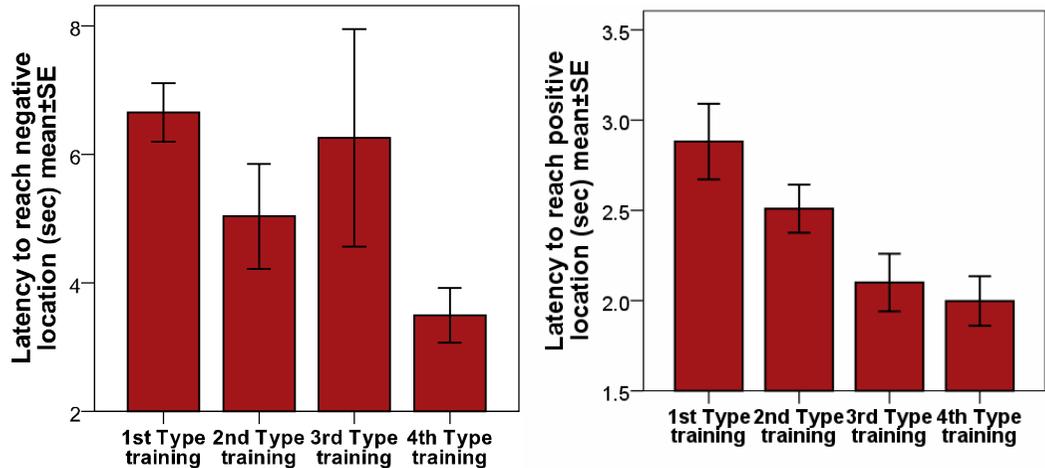


26. figure Histogram showing the number of trials necessary to fulfil criterion for dogs participating in the four different training types

Subjects in all groups approached with a shorter latency the positive location than the negative location ($t_{(81)} = 7.028$, $p < 0.001$), confirming that they successfully learned the task. However subjects in the four groups differed in their latency to approach both the positive ($F_{(3,58)} = 8.107$, $p < 0.001$) and the negative ($F_{(3,58)} = 5.666$, $p = 0.002$) location (Figure 27). Post hoc analysis (Tukey test) shows that the two training types using an identical methodology (1st & 2nd type) did not differ in the latency to approach the positive ($p = 0.346$) and the negative ($p = 0.378$) locations. Subjects in the 3rd training type reached the positive location with a shorter latency, than subjects in the 1st training type ($p = 0.020$), while they reached the negative location with a longer latency, than subjects in the 4th training type ($p = 0.023$). Subjects in the 4th training type reached the positive location with a shorter latency, than subjects in the 1st ($p < 0.001$) and 2nd ($p = 0.027$) training type while reached the negative location with a shorter latency, than subjects in the 3rd training type ($p = 0.023$).

These results suggest that minor differences in the training method can result in differences in subjects' performance. However if the test is carried out by two experimenters but in an identical way, than the same performance can be observed. Differences in the performance of the subjects in the four groups can be attributed to many of the subtle methodological differences, but the difference patterns are indicative of the importance of some methodological differences. The results show that latencies for the positive trials are higher in the 1st and 2nd

training types when subjects participated in other tasks before the Cognitive Bias test and were thus more tired. Latencies for the negative location in the 1st, 2nd and 3rd training types were higher and showed more variance, than in the 4th training type suggesting that the owner giving a command at the beginning of the trial might motivate dogs to approach the empty food bowl. Alternatively or in parallel dogs might take more (and a more variable amount of) time reaching the food bowl once they see that it is empty thus measuring the latency until the dog touches the bowl or goes within 10 cm might contribute to this difference.



27. figure Subjects' latencies to reach the positive and negative locations in the four training types; mean±SD. Please note that the latencies in the positive and negative trials differ considerably, thus the y axis are differently scaled.

Study II.

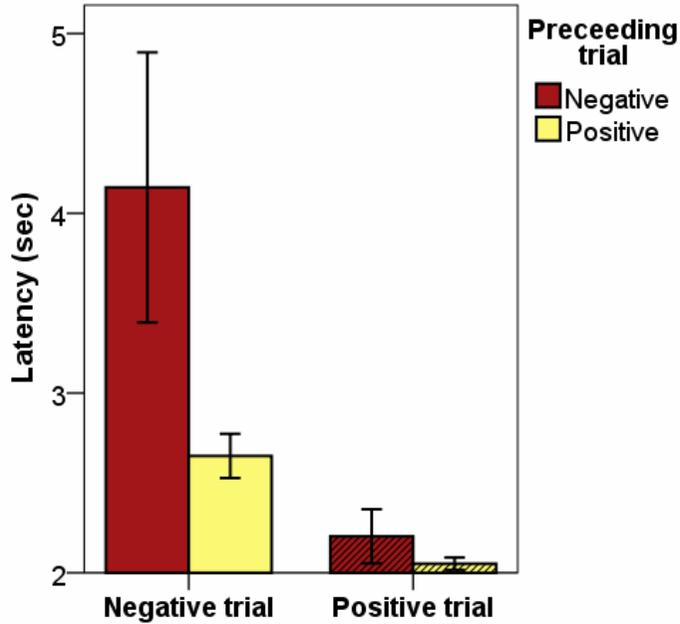
Methods

An additional group of dogs was tested with the 4th training type using a sample size (N=48), that allowed us to test the effect of additional factors on dogs' performance in the cognitive bias task. This training type employed a fix order of positive/negative trials, thus allowed us to test for the effect of preceding trials on latency to approach the food bowl besides the effects that the type of the actual trial had (GLM with fixed factors: actual trial positive/negative, preceding trial positive/negative). Furthermore inspired by some recent findings indicating that positive/negative emotions and thus approach/withdrawal behaviours are lateralized in dogs (Quaranta et al. 2007; Siniscalchi et al. 2010, 2013; Artelle et al. 2011; Nagasawa et al. 2013) we also aimed to test whether the positive/negative location being at the left/right side had an influence on the number of trials dogs needed to reach criteria (independent samples t-test) or on the difference between the latency to reach the positive vs. the negative location (independent samples t-test).

Results

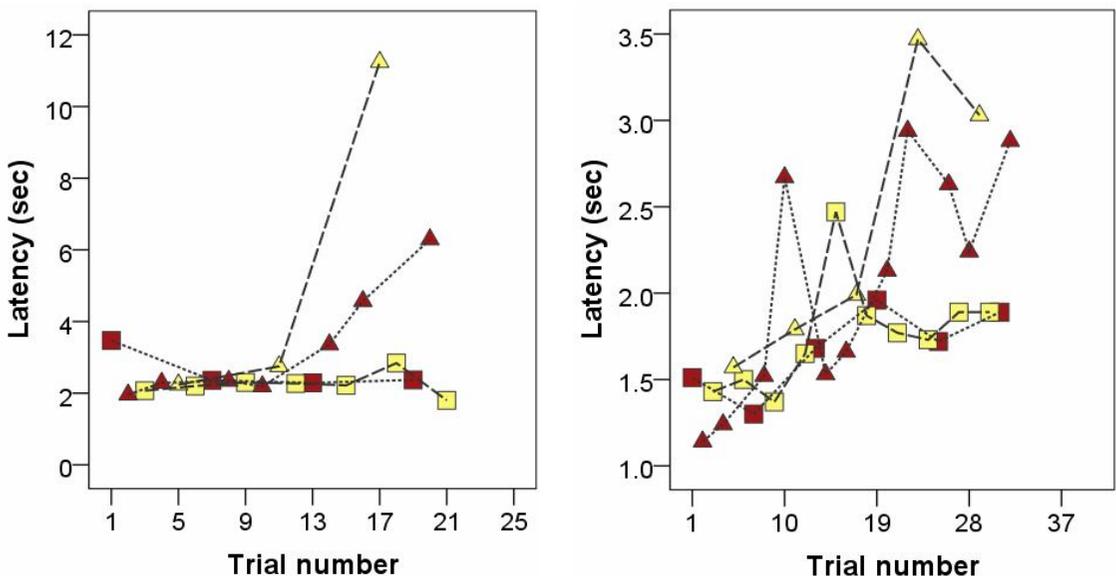
Although individual learning curves varied greatly (data from four individuals is shown in Figure 29 for illustrative purposes), the general tendency was that both the actual positive/negative trial ($F_{(1)}=21.567$, $p<0.001$) and the preceding positive/negative trial ($F_{(1)}=9.061$, $p=0.005$) had an effect on subjects' latency to approach the food bowl. There was a significant interaction among the effect of actual × preceding trials ($F_{(1)}=6.007$, $p=0.021$)

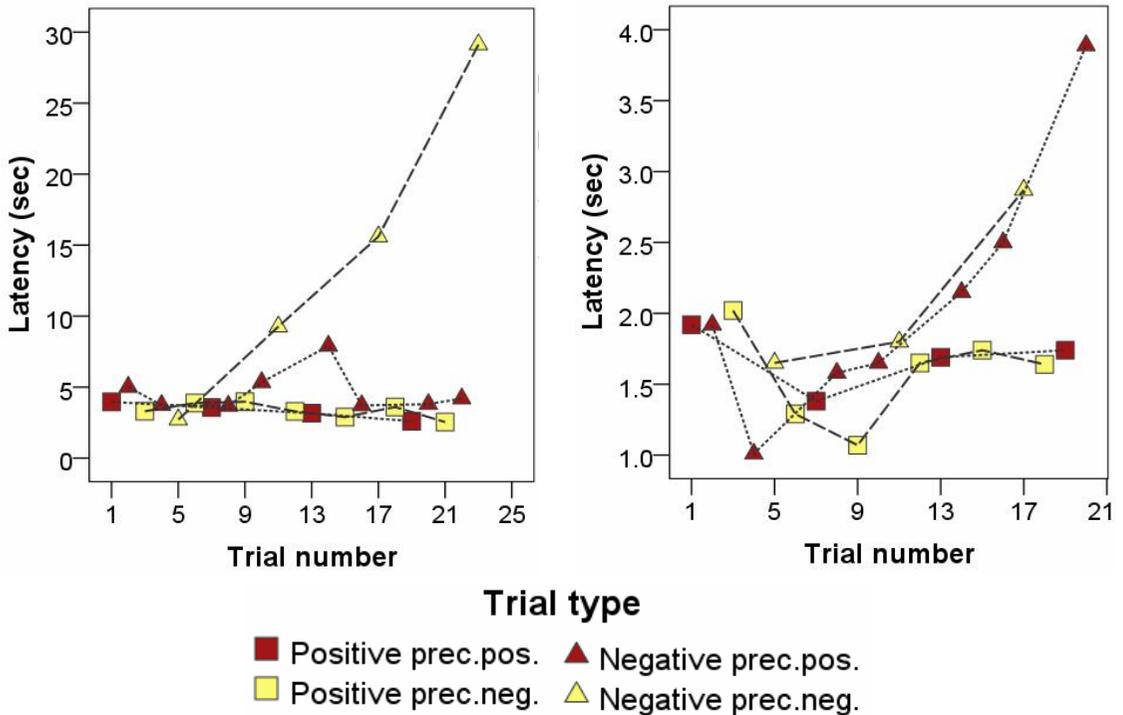
showing that a preceding negative trial had a more pronounced impact on the latency of a negative trial than on the latency of a positive trial (Figure 28).



28. figure The effect of the preceding (positive/negative) and the actual (positive/negative) trial type; mean±SD

There was no effect of the positive/negative side being left/right neither on the number of trials subjects needed to reach criteria ($t_{(46)}=0.474$, $p=0.637$) nor on the difference between the latency to reach the negative compared to the positive location ($t_{(46)}=0.731$, $p=0.468$). This contradicts to previous findings indicating that positive/negative emotions associated with approach/withdraw behaviours are lateralized in dogs (e.g. Quaranta et al. 2007; Artelle et al. 2011), but is in agreement with the results of Nagasawa et al. (2013) who found left facial lateralization for positive social (i.e. the owner), but not non-social (i.e. toys) stimuli.





29. figure Illustrative examples for individual latencies to approach the food bowl as a function of actual (positive/negative) × preceding (positive/negative) trials. Note that running speed varies greatly among individual dogs, thus the y axis (latency to approach the food bowl) is differently scaled for each graph. The number of trials to criterion also varies among individuals, thus the x axis is also scaled for each graph.

Discussion

Our result showed that subtle variations we applied in the training protocol of a discrimination learning task did not significantly influence the performance of dogs (the number of trials necessary to fulfil criterion), however the latency to reach the food bowl differed among training types. This suggests that the discrimination training task, that is an inherent part of the widely used Cognitive Bias test, is sensitive to the involuntary differences that inevitably exist between studies. Furthermore the fact that besides the actual information provided in each trial the type (positive/negative) of the preceding trial also influenced subjects' latency to approach also warn us to control for – or at least report – such methodological differences. We should also note, that when the same training protocol was used by two different experimenters (1st & 2nd types), then dogs behaved in the same way (both with respect to training criteria and latencies to reach the food bowl). This suggests that the discrimination training task is robust and replicable when carefully controlling for methodological details.

It is somewhat surprising that dogs participating in the socially aided trainings (1st, 2nd & 4th types) – where social reinforcement from the experimenter (happy/sad expression) was also included besides the food bowl being empty/baited – did not reach learning criterion in a reduced number of trials compared to the “normal” training group (3rd type). It is widely known that dogs are sensitive to human social cues including emotional expressions (Custance & Mayer 2012; Merola et al. 2012), that would make one expect that such cues help learning. However there is also evidence that food is a much stronger reinforcement for canines, than

human interaction (Feuerbacher & Wynne 2012), that is consistent with our findings. However similarly to Pongrácz et al. (2013) we did not find any indications that the quality of the food reward (sausage in 1st & 2nd type vs. dry food in 3rd & 4th type) would have affected subjects performance either.

We found that subjects participating in training procedures where the owner was not allowed to talk to the dog (1st, 2nd & 3rd types) tended to approach the empty but not the baited food bowl with higher latency compared to the group where the owner was allowed to give one command at the beginning of the trials in order to encourage the dog to search (4th type). A further common difference is in the latency criterion (dogs approached but at first did not touch the empty bowl).

Previous research has warned already against uncontrolled or unreported methodological details in dog cognition research such as the rearing history of the animals (Miklósi & Topál 2011), the presence/absence or the behaviour of the owner during the test (Kis et al. 2012a; Horn et al. 2013) or the test being carried out indoors/outdoors (Udell & Wynne 2011). Here we show that subtle differences in the training protocol of a discrimination learning task did influence the behaviour of dogs, although not substantially. However in cognition research – if significant – minor differences in subjects' responses (e.g. less than 100 milliseconds difference in the fixation time in case of an eye-tracking study (Somppi et al. 2012) investigating image processing) are often interpreted as evidence for a complex cognitive skill. Thus the current findings underline the importance of standard protocols being reported in full detail for the Cognitive Bias and possibly other tests measuring cognitive capabilities.

Furthermore our results confirm previous assumptions (Burman et al. 2011) that the Cognitive Bias approach can be used for dogs, as our subjects learned a left/right discrimination in a reasonable amount of trials, thus fulfilled the prerequisites for a Cognitive Bias test. Although the present findings warn for the possible effect of different training protocols, there is no evidence yet that latency in the training trials would be related to response to ambiguous stimuli in the test trials. However as the widely used “optimism/pessimism” score is calculated from the latencies to the positive, negative and ambivalent locations in the test trials, methodological differences – especially whether the last training trial preceding the test trials is positive or negative – might have a substantial effect.

Acknowledgement

I never would have imagined, until I got to this point, that writing an acknowledgement is one of the hardest tasks during the preparation of a dissertation. When looking back to the past few years that have led to this thesis, I feel that the people I am most grateful to are members of my family: my husband, my parents and eventually my entire family; but I find it inappropriate to start the acknowledgement with them first because giving the reasons for my gratitude would be too personal for anyone to read, and second because they were not directly involved in my scientific work. The one person who helped most with my thesis work is of course my supervisor, but she told me at the very beginning of our relationship that she did not want me to thank her in acknowledgements of thesis works because she was anyway mentioned in the front page, and because she considered helping me part of her job as supervisor. With this said I would like to thank all those colleagues who were co-authors of my publications for contributing to this thesis in a substantial way. Finally, I would like to thank *You* for reading my thesis, this probably means that you are interested in my work and have helped or will help me in some way.

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Ethics statement

All research reported in this thesis was conducted in accordance with the laws of the country in which it was carried out. Specific legislations, ethics committees and/or ethical approval reference numbers are provided in the papers referenced in each chapter.

References

- Amico, J. A., Johnston, J. M. & Vagnucci, A. H.** 1994. Suckling-induced attenuation of plasma cortisol concentrations in postpartum lactating women. *Endocrine Research*, **20**, 79–87.
- Andari, E., Duhamel, J.-R., Zalla, T., Herbrecht, E., Leboyer, M. & Sirigu, A.** 2010. Promoting social behavior with oxytocin in high-functioning autism spectrum disorders. *Proceedings of the National Academy of Sciences of the United States of America*, **107**, 4389–94.
- Andics, A., Gácsi, M., Faragó, T., Kis, A. & Miklósi, Á.** 2014. Dog-human brain parallels in voice processing: a comparative fMRI study. *Current Biology*, **24**, 574–8.
- Arkin, R. C., Fujita, M., Takagi, T. & Hasegawa, R.** 2003. An ethological and emotional basis for human–robot interaction. *Robotics and Autonomous Systems*, **42**, 191–201.
- Artelle, K. A., Dumoulin, L. K. & Reimchen, T. E.** 2011. Behavioural responses of dogs to asymmetrical tail wagging of a robotic dog replica. *Laterality*, **16**, 129–35.
- Aviezer, H., Bentin, S., Hassin, R. R., Meschino, W. S., Kennedy, J., Grewal, S., Esmail, S., Cohen, S. & Moscovitch, M.** 2009. Not on the face alone: perception of contextualized face expressions in Huntington’s disease. *Brain*, **132**, 1633–44.
- Baillargeon, R., Spelke, E. S. & Wasserman, S.** 1985. Object permanence in five-month-old infants. *Cognition*, **20**, 191–208.
- Bales, K. L. & Carter, C. S.** 2003. Developmental exposure to oxytocin facilitates partner preferences in male prairie voles (*Microtus ochrogaster*). *Behavioral Neuroscience*, **117**, 854–9.
- Bard, K. A. & Vaclair, J.** 1984. The communicative context of object manipulation in ape and human adult-infant pairs. *Journal of Human Evolution*, **13**, 181–190.
- Baron-Cohen, S., Wheelwright, S., Hill, J., Raste, Y. & Plumb, I.** 2001. The “Reading the Mind in the Eyes” Test revised version: a study with normal adults, and adults with Asperger syndrome or high-functioning autism. *Journal of Child Psychology and Psychiatry*, **42**, 241–51.
- Barraza, J. A., McCullough, M. E., Ahmadi, S. & Zak, P. J.** 2011. Oxytocin infusion increases charitable donations regardless of monetary resources. *Hormones and Behavior*, **60**, 148–51.
- Barrett, J. C., Fry, B., Maller, J. & Daly, M. J.** 2005. Haploview: analysis and visualization of LD and haplotype maps. *Bioinformatics*, **21**, 263–5.
- Bartneck, C.** 2001. How Convincing is Mr. Data’s Smile: Affective Expressions of Machines. *User Modeling and User-Adapted Interaction*, **11**, 279–95.
- Bartneck, C., Reichenbach, J. & Breemen, A. Van.** 2004. In your face, robot! The influence of a character’s embodiment on how users perceive its emotional expressions. In: *Proceedings of Design and Emotion*, Ankara.
- Bartz, J. A., Zaki, J., Bolger, N. & Ochsner, K. N.** 2011. Social effects of oxytocin in humans: context and person matter. *Trends in Cognitive Sciences*, **15**, 301–9.
- Bateson, M. & Matheson, S. M.** 2007. Performance on a categorisation task suggests that removal of environmental enrichment induces “pessimism” in captive European starlings (*Sturnus vulgaris*). *Animal Welfare*, **16**, 33–6.
- Bateson, M., Desire, S., Gartside, S. E. & Wright, G. A.** 2011. Agitated honeybees exhibit pessimistic cognitive biases. *Current Biology*, **21**, 1070–3.
- Baumgartner, T., Heinrichs, M., Vonlanthen, A., Fischbacher, U. & Fehr, E.** 2008. Oxytocin shapes the neural circuitry of trust and trust adaptation in humans. *Neuron*, **58**, 639–50.

- Beetz, A., Uvnäs-Moberg, K., Julius, H. & Kotrschal, K.** 2012. Psychosocial and psychophysiological effects of human-animal interactions: The possible role of oxytocin. *Frontiers in Psychology*, **3**, 1–15.
- Benjamini, Y., Drai, D., Elmer, G., Kafkafi, N. & Golani, I.** 2001. Controlling the false discovery rate in behavior genetics research. *Behavioural Brain Research*, **125**, 279–84.
- Berns, G. S., Brooks, A. & Spivak, M.** 2013. Replicability and heterogeneity of awake unrestrained canine fMRI responses. *PLoS ONE*, **8**, e81698.
- Billard, A.** 2003. Robota: Clever toy and educational tool. *Robotics and Autonomous Systems*, **42**, 259–69.
- Blanchard, R., McKittrick, C. & Blanchard, D.** 2001. Animal models of social stress: effects on behavior and brain neurochemical systems. *Physiology & Behavior*, **73**, 261–71.
- Boissy, A., Manteuffel, G., Jensen, M. B., Moe, R. O., Spruijt, B., Keeling, L. J., Winckler, C., Forkman, B., Dimitrov, I., Langbein, J., Bakken, M., Veissier, I. & Aubert, A.** 2007. Assessment of positive emotions in animals to improve their welfare. *Physiology & Behavior*, **92**, 375–97.
- Born, J., Lange, T., Kern, W., McGregor, G. P., Bickel, U. & Fehm, H. L.** 2002. Sniffing neuropeptides: a transnasal approach to the human brain. *Nature Neuroscience*, **5**, 514–16.
- Boyd, R. & Richerson, P. J.** 1988. An evolutionary model of social learning: the effects of spatial and temporal variation. In: *Social learning: Psychological and biological perspectives*, pp. 29–48. Hillsdale, NJ: Lawrence Erlbaum Associates.
- Bräuer, J., Call, J. & Tomasello, M.** 2004. Visual perspective taking in dogs (*Canis familiaris*) in the presence of barriers. *Applied Animal Behaviour Science*, **88**, 299–317.
- Bräuer, J., Kaminski, J., Riedel, J., Call, J. & Tomasello, M.** 2006. Making inferences about the location of hidden food: social dog, causal ape. *Journal of Comparative Psychology*, **120**, 38–47.
- Breazeal, C.** 2002. *Designing sociable robots*. Cambridge: MIT Press.
- Breazeal, C.** 2003. Emotion and sociable humanoid robots. *International Journal of Human-Computer Studies*, **59**, 119–55.
- Brosnan, S. F.** 2011. A Hypothesis of the Co-evolution of cooperation and responses to inequity. *Frontiers in Neuroscience*, **5**, 43.
- Burling, R., Armstrong, D. F., Blount, B. G., Callaghan, C. A., Foster, L., King, B. J., Parker, S. T., Sakura, O., Stokoe, W. C., Wallman, J., Whiten, A., Wilcox, S. & Wynn, T.** 1993. Primate calls, human language, and nonverbal communication. *Current Anthropology*, **34**, 25–53.
- Burman, O., Parker, R. M. a, Paul, E. S. & Mendl, M.** 2009. Anxiety-induced cognitive bias in non-human animals. *Physiology & Behavior*, **98**, 345–50.
- Burman, O., McGowan, R., Mendl, M., Norling, Y., Paul, E., Rehn, T. & Keeling, L.** 2011. Using judgement bias to measure positive affective state in dogs. *Applied Animal Behaviour Science*, **132**, 160–8.
- Byrne, R. W.** 2003. Imitation as behaviour parsing. *Philosophical Transactions of the Royal Society of London. Series B, Biological sciences*, **358**, 529–36.
- Caldwell, C. a & Whiten, A.** 2003. Scrounging facilitates social learning in common marmosets, *Callithrix jacchus*. *Animal Behaviour*, **65**, 1085–92.

- Campbell, A.** 2010. Oxytocin and human social behavior. *Personality and Social Psychology Review*, **14**, 281–95.
- Cañamero, L. & Fredslund, J.** 2000. How does it feel? Emotional interaction with a humanoid lego robot. In: *Intelligent Agents: The Human in the Loop*, pp. 23–8.
- Caro, T. M. & Hauser, M. D.** 1992. Is there teaching in nonhuman animals? *Quarterly Review of Biology*, **67**, 151–74.
- Carroll, J. M. & Russell, J. A.** 1996. Do facial expressions signal specific emotions? Judging emotion from the face in context. *Journal of Personality and Social Psychology*, **70**, 205–18.
- Carter, C. S.** 2014. Oxytocin pathways and the evolution of human behavior. *Annual Review of Psychology*, **65**, 17–39.
- Carver, C. S., Scheier, M. F. & Segerstrom, S. C.** 2010. Optimism. *Clinical Psychology Review*, **30**, 879–889.
- Chabris, C. F., Hebert, B. M., Benjamin, D. J., Beauchamp, J., Cesarini, D., van der Loos, M., Johannesson, M., Magnusson, P. K. E., Lichtenstein, P., Atwood, C. S., Freese, J., Hauser, T. S., Hauser, R. M., Christakis, N. & Laibson, D.** 2012. Most reported genetic associations with general intelligence are probably false positives. *Psychological Science*, **23**, 1314–23.
- Chase, K., Jones, P. G., Martin, A., Ostrander, E. a & Lark, K. G.** 2009. Genetic mapping of fixed phenotypes: disease frequency as a breed characteristic. *The Journal of Heredity*, **100**, S37–S41.
- Chen, F. S., Barth, M. E., Johnson, S. C. S. L. & Gotlib, I. H.** 2011. Oxytocin receptor (OXTR) polymorphisms and attachment in human infants. *Frontiers in Psychology*, **2**, 200.
- Chiodera, P. & Salvarani, C.** 1991. Relationship between plasma profiles of oxytocin and adrenocorticotrophic hormone during suckling or breast stimulation in women. *Hormone Research in Pediatrics*, **35**, 119–23.
- Cornelis, M. C., Glymour, M. M., Chang, S.-C., Tchetgen, E. J. T., Liang, L., Koenen, K. C., Kang, J. H., Pasquale, L. R., Rimm, E. B., Kawachi, I. & Kubzansky, L. D.** 2012. Oxytocin receptor (OXTR) is not associated with optimism in the Nurses' Health Study. *Molecular Psychiatry*, **17**, 1157–9.
- Crockford, C., Wittig, R. M., Langergraber, K., Ziegler, T. E., Zuberbühler, K. & Deschner, T.** 2013. Urinary oxytocin and social bonding in related and unrelated wild chimpanzees. *Proceedings of the Royal Society B: Biological Sciences*, **280**, 20122765.
- Cummings, E. M. & Bjork, E. L.** 1983. Search behavior on multi-choice hiding tasks: Evidence for an objective conception of space in infancy. *International Journal of Behavioral Development*, **6**, 71–87.
- Custance, D. & Mayer, J.** 2012. Empathic-like responding by domestic dogs (*Canis familiaris*) to distress in humans: an exploratory study. *Animal Cognition*, **15**, 851–859.
- Csányi, V.** 2000. The 'human behavior-complex' and the compulsion of communication: Key factors of human evolution. *Semiotica*, **128**, 45–60.
- Csányi, V.** 2003. Reconstruction of the major factors in the evolution of human behavior. *Praehistoria*, **4-5**, 1–12.
- Csibra, G.** 2007. Teachers in the wild. *Trends in Cognitive Sciences*, **11**, 95–96.
- Csibra, G.** 2010. Recognizing Communicative Intentions in Infancy. *Mind & Language*, **25**, 141–68.

- Csibra, G. & Gergely, G.** 2006. Social learning and social cognition: The case for pedagogy. In: *Processes of Change in Brain and Cognitive Development. Attention and Performance, XXI.*, (Ed. by Y. Munakata & M. Johnson), pp. 249–74. Oxford: Oxford University Press.
- Csibra, G. & Gergely, G.** 2009. Natural pedagogy. *Trends in cognitive sciences*, **13**, 148–53.
- Davis, K. M. & Burghardt, G. M.** 2011. Turtles (*Pseudemys nelsoni*) learn about visual cues indicating food from experienced turtles. *Journal of Comparative Psychology*, **125**, 404–410.
- Dawson, B. V. & Foss, B. M.** 1965. Observational learning in Budgerigars. *Animal Behaviour*, **13**, 470–4.
- De Blois, S. T., Novak, M. a & Bond, M.** 1998. Object permanence in orangutans (*Pongo pygmaeus*) and squirrel monkeys (*Saimiri sciureus*). *Journal of Comparative Psychology*, **112**, 137–52.
- De Gelder, B.** 2009. Why bodies? Twelve reasons for including bodily expressions in affective neuroscience. *Philosophical Transactions of the Royal Society of London. Series B, Biological sciences*, **364**, 3475–84.
- Dehaene, S. & Cohen, L.** 2007. Cultural recycling of cortical maps. *Neuron*, **56**, 384–98.
- Deisseroth, K.** 2011. Optogenetics. *Nature Methods*, **8**, 26–9.
- Dell’Mour, V., Range, F. & Huber, L.** 2009. Social learning and mother’s behavior in manipulative tasks in infant marmosets. *American Journal of Primatology*, **71**, 503–9.
- Diamond, A.** 1985. Development of the ability to use recall to guide action, as indicated by infants’ performance on AB. *Child Development*, **56**, 868–83.
- Diederich, C. & Giffroy, J.** 2006. Behavioural testing in dogs: A review of methodology in search for standardisation. *Applied Animal Behaviour Science*, **97**, 51–72.
- Domes, G., Heinrichs, M., Michel, A., Berger, C. & Herpertz, S. C.** 2007a. Oxytocin improves “mind-reading” in humans. *Biological Psychiatry*, **61**, 731–3.
- Domes, G., Heinrichs, M., Gläscher, J., Büchel, C., Braus, D. F. & Herpertz, S. C.** 2007b. Oxytocin attenuates amygdala responses to emotional faces regardless of valence. *Biological Psychiatry*, **62**, 1187–90.
- Donaldson, Z. R. & Young, L. J.** 2008. Oxytocin, vasopressin, and the neurogenetics of sociality. *Science*, **322**, 900–4.
- Doody, J. S., Burghardt, G. M. & Dinets, V.** 2012. Breaking the social – non-social dichotomy: A role for reptiles in vertebrate social behavior research? *Ethology*, **119**, 95–103.
- Doyle, R. E., Vidal, S., Hinch, G. N., Fisher, A. D., Boissy, A. & Lee, C.** 2010. The effect of repeated testing on judgement biases in sheep. *Behavioural Processes*, **83**, 349–52.
- Dumas, M.-C.** 1992. Object permanence in cats (*Felis catus*): an ecological approach to the study of invisible displacements. *Journal of Comparative Psychology*, **106**, 404–10.
- Ekman, P.** 1992. Are there basic emotions? *Cognition & Emotion*, **99**, 550–3.
- Elfenbein, H. A. & Ambady, N.** 2002. On the universality and cultural specificity of emotion recognition: A meta-analysis. *Psychological Bulletin*, **128**, 203–35.
- Erdőhegyi, Á., Topál, J., Virányi, Z. & Miklósi, Á.** 2007. Dog-logic: inferential reasoning in a two-way choice task and its restricted use. *Animal Behaviour*, **74**, 725–37.

- Faragó, T., Miklósi, Á., Korcsok, B., Száraz, J. & Gácsi, M.** 2014a. Social behaviours in dog-owner interactions can serve as a model for designing social robots. *Interaction Studies*, accepted as a target article
- Faragó, T., Andics, A., Devecseri, V., Kis, A., Gácsi, M., Ádám, M. & Miklósi, Á.** 2014b. Humans rely on the same rules to assess emotional valence and intensity in conspecific and dog vocalizations. *Biology Letters*, **10**, 20130926.
- Feistner, A. T. C. & Price, E. C.** 1991. Food offering in new world primates: two species added. *Folia Primatologica*, **3**, 165–8.
- Ferguson, J. N., Young, L. J. & Insel, T. R.** 2002. The neuroendocrine basis of social recognition. *Frontiers in Neuroendocrinology*, **23**, 200–4.
- Ferrari, P. F., Paukner, A., Ionica, C. & Suomi, S. J.** 2009. Reciprocal face-to-face communication between rhesus macaque mothers and their newborn infants. *Current Biology*, **19**, 1768–72.
- Feuerbacher, E. N. & Wynne, C. D. L.** 2012. Relative efficacy of human social interaction and food as reinforcers for domestic dogs and hand-reared wolves. *Journal of the experimental analysis of behavior*, **98**, 105–29.
- Fiorito, G. & Scotto, P.** 1992. Observational Learning in *Octopus vulgaris*. *Science*, **256**, 545–7.
- Fiset, S.** 2010. Comment on “Differential sensitivity to human communication in dogs, wolves, and human infants”. *Science*, **329**, 142b.
- Fiset, S. & Leblanc, V.** 2007. Invisible displacement understanding in domestic dogs (*Canis familiaris*): the role of visual cues in search behavior. *Animal Cognition*, **10**, 211–24.
- Fox, M. W.** 1971. Socio-infantile and socio-sexual signals in Canids: A comparative and ontogenetic study. *Zeitschrift fuer Tierpsychologie*, **28**, 185–210.
- Freidin, E., Putrino, N., D’Orazio, M. & Bentosela, M.** 2013. Dogs’ eavesdropping from people’s reactions in third party interactions. *PLoS ONE*, **8**, e79198.
- Gácsi, M., Topál, J., Miklósi, Á., Dóka, A. & Csányi, V.** 2001. Attachment behavior of adult dogs (*Canis familiaris*) living at rescue centers: Forming new bonds. *Journal of Comparative Psychology*, **115**, 423–31.
- Gácsi, M., Topál, J., Csányi, V., Győri, B., Miklósi, Á., Virányi, Z. & Kubinyi, E.** 2005. Species-specific differences and similarities in the behavior of hand-raised dog and wolf pups in social situations with humans. *Developmental Psychobiology*, **47**, 111–22.
- Gácsi, M., Győri, B., Virányi, Z., Kubinyi, E., Range, F., Belényi, B. & Miklósi, Á.** 2009. Explaining dog wolf differences in utilizing human pointing gestures: selection for synergistic shifts in the development of some social skills. *PLoS ONE*, **4**, e6584.
- Gácsi, M., Szakadát, S. & Miklósi, Á.** 2013a. Assistance dogs provide a useful behavioral model to enrich communicative skills of assistance robots. *Frontiers in Psychology*, **4**, 971.
- Gácsi, M., Maros, K., Sernkvist, S., Faragó, T. & Miklósi, Á.** 2013b. Human analogue safe haven effect of the owner: Behavioural and heart rate response to stressful social stimuli in dogs. *PLoS ONE*, **8**, e58475.
- Gagnon, S. & Doré, F. Y.** 1992. Search behavior in various breeds of adult dogs (*Canis familiaris*): Object permanence and olfactory cues. *Journal of Comparative Psychology*, **106**, 58–68.

- Garrett, A. S., Menon, V., Mackenzie, K. & Reiss, A. L.** 2004. Here's Looking at You, Kid. Neural systems underlying face and gaze processing in fragile X syndrome. *Archives of General Psychiatry*, **61**, 281–8.
- Gillath, O., Shaver, P. R., Baek, J.-M. & Chun, D. S.** 2008. Genetic correlates of adult attachment style. *Personality & Social Psychology Bulletin*, **34**, 1396–405.
- Gimpl, G. & Fahrenholz, F.** 2001. The oxytocin receptor system: structure, function, and regulation. *Physiological Reviews*, **81**, 629–83.
- Gockley, R., Bruce, A., Forlizzi, J., Michalowski, M., Mundell, A., Rosenthal, S., Sellner, B., Simmons, R., Snipes, K. & Schultz, A. C.** 2005. Designing robots for long-term social interaction. In: *International Conference on Intelligent Robots and Systems*, pp. 2199–204.
- Gómez, J.-C. & Go, J.** 2005. Species comparative studies and cognitive development. *Trends in Cognitive Sciences*, **9**, 118–25.
- Goodson, J. L. & Bass, A. H.** 2001. Social behavior functions and related anatomical characteristics of vasotocin/vasopressin systems in vertebrates. *Brain Research Reviews*, **35**, 246–65.
- Gosling, S. D., Kwan, V. S. Y. & John, O. P.** 2003. A dog's got personality: a cross-species comparative approach to personality judgments in dogs and humans. *Journal of Personality and Social Psychology*, **85**, 1161–9.
- Gratch, G., Appel, K. J., Evans, W. F., LeCompte, G. K. & Wright, N. A.** 1974. Piaget's stage IV object concept error: Evidence of forgetting or object conception? *Child Development*, **45**, 71–7.
- Guastella, A. J., Mitchell, P. B. & Dadds, M. R.** 2008a. Oxytocin increases gaze to the eye region of human faces. *Biological Psychiatry*, **63**, 3–5.
- Guastella, A. J., Mitchell, P. B. & Mathews, F.** 2008b. Oxytocin enhances the encoding of positive social memories in humans. *Biological Psychiatry*, **64**, 256–8.
- Guastella, A. J., Hickie, I. B., McGuinness, M. M., Otis, M., Woods, E. a., Disinger, H. M., Chan, H.-K., Chen, T. F. & Banati, R. B.** 2013. Recommendations for the standardisation of oxytocin nasal administration and guidelines for its reporting in human research. *Psychoneuroendocrinology*, **38**, 612–25.
- Gutkowska, J. & Jankowski, M.** 2008. Oxytocin revisited: It is also a cardiovascular hormone. *Journal of the American Society of Hypertension*, **2**, 318–25.
- Gyuris, E., Feró, O., Tartally, A. & Barta, Z.** 2011. Individual behaviour in firebugs (*Pyrrhocoris apterus*). *Proceedings of the Royal Society B: Biological Sciences*, **278**, 628–633.
- Haller, J.** 2013. The neurobiology of abnormal manifestations of aggression – A review of hypothalamic mechanisms in cats, rodents, and humans. *Brain Research Bulletin*, **93**, 97–109.
- Halloy, J., Sempo, G., Caprari, G., Rivault, C., Asadpour, M., Tâche, F., Saïd, I., Durier, V., Canonge, S., Amé, J. M., Detrain, C., Correll, N., Martinoli, A., Mondada, F., Siegwart, R. & Deneubourg, J. L.** 2007. Social integration of robots into groups of cockroaches to control self-organized choices. *Science*, **318**, 1155–8.
- Harding, E. J., Paul, E. S. & Mendl, M.** 2004. Cognitive bias and affective state. *Nature*, **427**, 321.
- Hare, B. & Tomasello, M.** 2005. Human-like social skills in dogs? *Trends in Cognitive Sciences*, **9**, 439–44.
- Hare, B., Call, J., Agnetta, B. & Tomasello, M.** 2000. Chimpanzees know what conspecifics do and do not see. *Animal Behaviour*, **59**, 771–85.

- Hare, B., Call, J. & Tomasello, M.** 2001. Do chimpanzees know what conspecifics know? *Animal Behaviour*, **61**, 139–51.
- Hare, B., Brown, M., Williamson, C. & Tomasello, M.** 2002. The domestication of social cognition in dogs. *Science*, **298**, 1634–6.
- Hare, B., Plyusnina, I., Ignacio, N., Schepina, O., Stepika, A., Wrangham, R. & Trut, L. N.** 2005. Social cognitive evolution in captive foxes is a correlated by-product of experimental domestication. *Current Biology*, **15**, 226–30.
- Hartshorne, J. K.** 2008. Visual working memory capacity and proactive interference. *PLoS ONE*, **3**, e2716.
- Hecht, J., Miklósi, Á. & Gácsi, M.** 2012. Behavioral assessment and owner perceptions of behaviors associated with guilt in dogs. *Applied Animal Behaviour Science*, **139**, 134–42.
- Heinrichs, M. & Domes, G.** 2008. Neuropeptides and social behaviour: effects of oxytocin and vasopressin in humans. *Progress in Brain Research*, **170**, 337–50.
- Heinrichs, M. & Gaab, J.** 2007. Neuroendocrine mechanisms of stress and social interaction: implications for mental disorders. *Current Opinion in Psychiatry*, **20**, 158–62.
- Heinrichs, M., Baumgartner, T., Kirschbaum, C. & Ehlert, U.** 2003. Social support and oxytocin interact to suppress cortisol and subjective responses to psychosocial stress. *Biological Psychiatry*, **54**, 1389–98.
- Heinrichs, M., Dawans, B. Von, Domes, G. & von Dawans, B.** 2009. Oxytocin, vasopressin, and human social behavior. *Frontiers in Neuroendocrinology*, **30**, 548–57.
- Heinroth, O.** 1910. Beiträge zur Biologie, namentlich Ethologie und Psychologie der Anatiden. *Verh Int Ornithol Kongr*, **5**, 589–701.
- Hejjas, K., Vas, J., Topál, J., Szantai, E., Ronai, Z., Szekely, A., Kubinyi, E., Horváth, Z., Sasvari-Szekely, M. & Miklósi, Á.** 2007. Association of polymorphisms in the dopamine D4 receptor gene and the activity-impulsivity endophenotype in dogs. *Animal Genetics*, **38**, 629–33.
- Herman, L. M., Abichandani, S. L., Elhajj, a N., Herman, E. Y., Sanchez, J. L. & Pack, a a.** 1999. Dolphins (*Tursiops truncatus*) comprehend the referential character of the human pointing gesture. *Journal of Comparative Psychology*, **113**, 347–64.
- Hernádi, A., Miklósi, B., Kanizsár, O., Kis, A., Miklósi, Á. & Topál, J.** 2014. Oxytocin modulates how dogs (*Canis familiaris*) look at human emotional faces. An eye-tracking study. *Animal Cognition*, under review.
- Herrmann, E., Call, J., Hernández-Lloreda, M. V., Hare, B. & Tomasello, M.** 2007. Humans have evolved specialized skills of social cognition: the cultural intelligence hypothesis. *Science*, **317**, 1360–6.
- Heyes, C.** 1994. Social learning in animals: categories and mechanisms. *Biological Reviews*, **69**, 207–31.
- Heyes, C. & Ray, E. D.** 2002. Distinguishing intention-sensitive from outcome-sensitive imitation. *Developmental Science*, **5**, 34–6.
- Heyes, C., Huber, L., Gergely, G. & Brass, M.** 2009. Evolution, development and intentional control of imitation (special issue). *Philosophical Transactions of the Royal Society B: Biological Sciences*, **364**, 2291–443.

- Hol, T., Van den Berg, C., Van Ree, J. M. & Sprujit, B. M.** 1999. Isolation during the play period in infancy decreases adult social interactions in rats. *Behavioural Brain Research*, **100**, 91–7.
- Hollander, E., Bartz, J. A., Chaplin, W., Phillips, A., Sumner, J., Soorya, L., Anagnostou, E. & Wasserman, S.** 2007. Oxytocin increases retention of social cognition in autism. *Biological psychiatry*, **61**, 498–503.
- Horn, L., Huber, L. & Range, F.** 2013. The importance of the secure base effect for domestic dogs – Evidence from a manipulative problem-solving task. *PLoS ONE*, **8**, e65296.
- Horowitz, A.** 2009. Disambiguating the “guilty look”: Salient prompts to a familiar dog behaviour. *Behavioural Processes*, **81**, 447–52.
- Horowitz, A.** 2012. Fair is fine, but more is better: Limits to inequity aversion in the domestic dog. *Social Justice Research*, **25**, 195–212.
- Insel, T. R.** 2002. Social anxiety: from laboratory studies to clinical practice. *Biological Psychiatry*, **51**, 1–3.
- Insel, T. R. & Shapiro, L. E.** 1992. Oxytocin receptor distribution reflects social organization in monogamous and polygamous voles. *Proceedings of the National Academy of Sciences of the United States of America*, **89**, 5981–5.
- Jones, A. C. & Gosling, S. D.** 2005. Temperament and personality in dogs (*Canis familiaris*): A review and evaluation of past research. *Applied Animal Behaviour Science*, **95**, 1–53.
- Jones, T., Lawson, S. & Mills, D.** 2008a. Interaction with a zoomorphic robot that exhibits canid mechanisms of behaviour. *2008 IEEE International Conference on Robotics and Automation*, 2128–33.
- Jones, P. G., Chase, K., Martin, A., Davern, P., Ostrander, E. a & Lark, K. G.** 2008b. Single-nucleotide-polymorphism-based association mapping of dog stereotypes. *Genetics*, **179**, 1033–44.
- Kaminski, J.** 2009. Dogs (*Canis familiaris*) are adapted to receive human communication. In: *Neurobiology of “Umwelt”: How Living Beings Perceive the World*, (Ed. by A. Berthoz & Y. Christensen), pp. 103–107. Berlin Heidelberg: Springer-Verlag.
- Kaminski, J., Riedel, J., Call, J. & Tomasello, M.** 2005. Domestic goats, *Capra hircus*, follow gaze direction and use social cues in an object choice task. *Animal Behaviour*, **69**, 11–8.
- Kaminski, J., Schulz, L. & Tomasello, M.** 2012a. How dogs know when communication is intended for them. *Developmental Science*, **15**, 222–32.
- Kaminski, J., Pitsch, A. & Tomasello, M.** 2012b. Dogs steal in the dark. *Animal cognition*, 385–94.
- Kasper, C., Voelkl, B. & Huber, L.** 2008. Tolerated mouth-to-mouth food transfers in common marmosets. *Primates*, **49**, 153–6.
- Kätsyri, J., Klucharev, V., Frydrych, M. & Sams, M.** 2003. Identification of synthetic and natural emotional facial expressions. In: *International Conference on Audio-Visual Speech Processing (AVSP 2003)*, pp. 3–7. St. Jorioz.
- Kemp, A. H., Quintana, D. S., Kuhnert, R.-L., Griffiths, K., Hickie, I. B. & Guastella, A. J.** 2012. Oxytocin increases heart rate variability in humans at rest: Implications for social approach-related motivation and capacity for social engagement. *PLoS ONE*, **7**, e44014.

- Kirchhofer, K. K. C., Zimmermann, F., Kaminski, J. & Tomasello, M.** 2012. Dogs (*Canis familiaris*), but not chimpanzees (*Pan troglodytes*), understand imperative pointing. *PLoS ONE*, **7**, e30913.
- Kirkness, E. F., Bafna, V., Halpern, A. L., Levy, S., Remington, K., Rusch, D. B., Delcher, A. L., Pop, M., Wang, W., Fraser, C. M. & Venter, J. C.** 2003. The dog genome: survey sequencing and comparative analysis. *Science*, **301**, 1898–903.
- Kirsch, P., Esslinger, C., Chen, Q., Mier, D., Lis, S., Siddhanti, S., Gruppe, H., Mattay, V. S., Gallhofer, B. & Meyer-Lindenberg, A.** 2005. Oxytocin modulates neural circuitry for social cognition and fear in humans. *The Journal of Neuroscience*, **25**, 11489–93.
- Kis, A., Turcsán, B., Miklósi, Á. & Gácsi, M.** 2012a. The effect of the owner's personality on the behaviour of owner-dog dyads. *Interaction Studies*, **13**, 371–83.
- Kis, A., Topál, J., Gácsi, M., Range, F., Huber, L., Miklósi, Á. & Virányi, Z.** 2012b. Does the A-not-B error in adult pet dogs indicate sensitivity to human communication? *Animal Cognition*, **15**, 737–43.
- Kis, A., Kemerle, K., Hernádi, A. & Topál, J.** 2013. Oxytocin and social pretreatment have similar effects on processing of negative emotional faces in healthy adult males. *Frontiers in Psychology*, **4**, 1–9.
- Kis, A., Szakadát, S., Kovács, E., Gácsi, M., Simor, P., Gombos, F., Topál, J., Miklósi, Á. & Bódizs, R.** 2014. Development of a non-invasive polysomnography technique for dogs (*Canis familiaris*). *Physiology & Behavior*, under revision.
- Klausz, B., Kis, A., Persa, E. & Gácsi, M.** 2009. Human-directed aggression in shelter dogs: how to test for better prediction of outcomes. *Journal of Veterinary Behavior*, **4**, 78.
- Klausz, B., Kis, A., Persa, E., Miklósi, Á. & Gácsi, M.** 2014. A quick assessment tool for human-directed aggression in pet dogs. *Aggressive Behavior*, **40**, 178–88.
- Klein, E. D. & Zentall, T. R.** 2003. Imitation and affordance learning by pigeons (*Columba livia*). *Journal of Comparative Psychology*, **117**, 414–9.
- Koay, K. L., Lakatos, G., Syrdal, D. S., Gácsi, M., Bereczky, B., Dautenhahn, K., Miklósi, Á. & Walters, M. L.** 2013. Hey! There is someone at your door. A hearing robot using visual communication signals of hearing dogs to communicate intent. In: *Proceeding of the 2013 IEEE Symposium on Artificial Life*, pp. 90–97. Singapore.
- Konok, V., Dóka, A. & Miklósi, Á.** 2011. The behavior of the domestic dog (*Canis familiaris*) during separation from and reunion with the owner: A questionnaire and an experimental study. *Applied Animal Behaviour Science*, **135**, 300–8.
- Kosfeld, M., Heinrichs, M., Zak, P. J., Fischbacher, U. & Fehr, E.** 2005. Oxytocin increases trust in humans. *Nature*, **435**, 673–6.
- Kovács, S., Vincze, D., Gácsi, M., Miklósi, Á. & Korondi, P.** 2009. Interpolation based fuzzy automaton for human-robot interaction. In: *9th IFAC Symposium on Robot Control Nagarakawa Convention Center*, Gifu, Japan.
- Kubinyi, E., Turcsán, B. & Miklósi, Á.** 2009. Dog and owner demographic characteristics and dog personality trait associations. *Behavioural Processes*, **81**, 392–401.
- Kubinyi, E., Vas, J., Hejjas, K., Ronai, Z., Brúder, I., Turcsán, B., Sasvari-Szekely, M. & Miklósi, Á.** 2012. Polymorphism in the tyrosine hydroxylase (TH) gene is associated with activity-impulsivity in German Shepherd dogs. *PLoS ONE*, **7**, e30271.

- Kumashiro, M., Ishibashi, H., Itakura, S. & Iriki, A.** 2002. Bidirectional communication between a Japanese monkey and a human through eye gaze and pointing. *Cahiers de Psychologie Cognitive/Current Psychology of Cognition*, **21**, 3–32.
- Kumsta, R. & Heinrichs, M.** 2012. Oxytocin, stress and social behavior: neurogenetics of the human oxytocin system. *Current Opinion in Neurobiology*, 1–6.
- Kundey, S. M. a, De los Reyes, A., Royer, E., Molina, S., Monnier, B., German, R. & Coshun, A.** 2011. Reputation-like inference in domestic dogs (*Canis familiaris*). *Animal Cognition*, **14**, 291–302.
- Kupán, K., Miklósi, Á., Gergely, G. & Topál, J.** 2011. Why do dogs (*Canis familiaris*) select the empty container in an observational learning task? *Animal Cognition*, **14**, 259–68.
- Lakatos, G., Gácsi, M., Topál, J. & Miklósi, Á.** 2011. Comprehension and utilisation of pointing gestures and gazing in dog-human communication in relatively complex situations. *Animal Cognition*, **15**, 18–22.
- Landis, J. R. & Koch, G. G.** 1977. The measurement of observer agreement for categorical data. *Biometrics*, **33**, 159–74.
- Lee, H.-J., Macbeth, A. H., Pagani, J. H. & Young, W. S.** 2009. Oxytocin: the great facilitator of life. *Progress in Neurobiology*, **88**, 127–51.
- Lee, A. G., Cool, D. R., Grunwald, W. C., Neal, D. E., Buckmaster, C. L., Cheng, M. Y., Hyde, S. a, Lyons, D. M. & Parker, K. J.** 2011. A novel form of oxytocin in New World monkeys. *Biology Letters*, **7**, 584–7.
- Leite, I., Martinho, C. & Paiva, A.** 2008. Are emotional robots more fun to play with? In: *The 17th IEEE International Symposium*, pp. 77–82.
- Lessells, C. M. & Boag, P. T.** 1987. Unrepeatable repeatabilities. *The Auk*, **104**, 116–21.
- Li, H., Yeow, J. C. & Tan, K.** 2011. Towards an effective design of social robots. *International Journal of Social Robotics*, **3**, 333–5.
- Light, K. C., Grewen, K. M. & Amico, J. a.** 2005. More frequent partner hugs and higher oxytocin levels are linked to lower blood pressure and heart rate in premenopausal women. *Biological Psychology*, **69**, 5–21.
- Lischke, A., Berger, C., Prehn, K., Heinrichs, M., Herpertz, S. C. & Domes, G.** 2012. Intranasal oxytocin enhances emotion recognition from dynamic facial expressions and leaves eye-gaze unaffected. *Psychoneuroendocrinology*, **37**, 475–81.
- Lodé, T.** 1999. Comparative measurements of terrestrial and aquatic locomotion in *Mustela lutreola* and *Mustela putorius*. *Zeit fur Saugertier*, **64**, 110–5.
- Lodé, T.** 2008. Kin recognition versus familiarity in a solitary mustelid, the European polecat *Mustela putorius*. *Comptes Rendus Biologies*, **331**, 248–54.
- Longo, M. R. & Bertenthal, B. I.** 2006. Common coding of observation and execution of action in 9-month-old infants. *Infancy*, **10**, 43–59.
- Loughland, C. M., Williams, L. M. & Gordon, E.** 2002. Schizophrenia and affective disorder show different visual scanning behavior for faces: a trait versus state-based distinction? *Biological Psychiatry*, **52**, 338–48.

- Lucht, M. J., Barnow, S., Sonnenfeld, C., Rosenberger, A., Grabe, J. H., Schroeder, W., Völzke, H., Freyberger, H. J., Herrmann, F. H., Kroemer, H. & Roszkopf, D.** 2009. Associations between the oxytocin receptor gene (OXTR) and affect, loneliness and intelligence in normal subjects. *Progress in Neuropsychopharmacology & Biological Psychiatry*, **33**, 860–6.
- Macdonald, K. & Macdonald, T. M.** 2010. The peptide that binds: a systematic review of oxytocin and its prosocial effects in humans. *Harvard Review of Psychiatry*, **18**, 1–21.
- MacDorman, K. F. & Ishiguro, H.** 2006. The uncanny advantage of using androids in cognitive and social science research. *Interaction Studies*, **7**, 297–337.
- MacDorman, K. F., Green, R. D., Ho, C.-C. & Koch, C. T.** 2009. Too real for comfort? Uncanny responses to computer generated faces. *Computers in Human Behavior*, **25**, 695–710.
- Maros, K., Gácsi, M. & Miklósi, Á.** 2008. Comprehension of human pointing gestures in horses (*Equus caballus*). *Animal Cognition*, **11**, 457–66.
- Marshall-Pescini, S., Passalacqua, C., Valsecchi, P. & Prato-Previde, E.** 2010. Comment on “Differential sensitivity to human communication in dogs, wolves, and human infants.” *Science*, **329**, 142c.
- Marshall-Pescini, S., Passalacqua, C., Ferrario, A., Valsecchi, P. & Prato-Previde, E.** 2011. Social eavesdropping in the domestic dog. *Animal Behaviour*, **81**, 1–28.
- Marx, P., Arany, A., Ronai, Z., Antal, P. & Sasvari-Szekely, M.** 2011. Genetic variability of the oxytocin receptor: an in silico study. *Neuropsychopharmacologia Hungarica*, **13**, 139–44.
- McGonigle, P.** 2014. Animal models of CNS disorders. *Biochemical Pharmacology*, **87**, 140–9.
- McGraw, L. A., Davis, J. K., Thomas, P. J., Young, L. J. & Thomas, J. W.** 2012. BAC-based sequencing of behaviorally-relevant genes in the prairie vole. *PLoS ONE*, **7**, e29345.
- Meeren, H. K. M., van Heijnsbergen, C. C. R. J. & de Gelder, B.** 2005. Rapid perceptual integration of facial expression and emotional body language. *Proceedings of the National Academy of Sciences of the United States of America*, **102**, 16518–23.
- Meltzoff, A. N.** 1988. The human infant as homo imitans. In: *Social learning: Psychological and biological perspectives*, (Ed. by T. Zental & B. Galef Jr), pp. 319–341. Erlbaum, Hillsdale.
- Mendes, N. & Huber, L.** 2004. Object permanence in common marmosets (*Callithrix jacchus*). *Journal of Comparative Psychology*, **118**, 103–112.
- Mendl, M., Burman, O., Parker, R. M. A. & Paul, E. S.** 2009. Cognitive bias as an indicator of animal emotion and welfare: Emerging evidence and underlying mechanisms. *Applied Animal Behaviour Science*, **118**, 161–81.
- Mendl, M., Brooks, J., Basse, C., Burman, O., Paul, E., Blackwell, E. & Casey, R.** 2010. Dogs showing separation-related behaviour exhibit a “pessimistic” cognitive bias. *Current Biology*, **20**, R839–40.
- Merola, I., Prato-Previde, E. & Marshall-Pescini, S.** 2012. Dogs’ social referencing towards owners and strangers. *PLoS ONE*, **7**, e47653.
- Miklósi, Á.** 2007. *Dog behaviour, evolution and cognition*. Oxford University Press.
- Miklósi, Á. & Gácsi, M.** 2012. On the utilisation of social animals as a model for social robotics. *Frontiers in Psychology*, **3**, 1–10.
- Miklósi, Á. & Topál, J.** 2011. On the hunt for the gene of perspective taking: Pitfalls in methodology. *Learning & Behavior*, **39**, 310–3.

- Miklósi, Á. & Topál, J.** 2013. What does it take to become “best friends”? Evolutionary changes in canine social competence. *Trends in Cognitive Sciences*, **17**, 287–94.
- Miklósi, Á., Kubinyi, E., Topál, J., Gácsi, M., Virányi, Z. & Csányi, V.** 2003. A simple reason for a big difference: wolves do not look back at humans, but dogs do. *Current Biology*, **13**, 763–766.
- Miklósi, Á., Topál, J. & Csányi, V.** 2004. Comparative social cognition: what can dogs teach us? *Animal Behaviour*, **67**, 995–1004.
- Miklósi, Á., Pongrácz, P., Lakatos, G., Topál, J. & Csányi, V.** 2005. A comparative study of the use of visual communicative signals in interactions between dogs (*Canis familiaris*) and humans and cats (*Felis catus*) and humans. *Journal of Comparative Psychology*, **119**, 179–86.
- Miklósi, Á., Topál, J. & Csányi, V.** 2007. Big thoughts in small brains? Dogs as a model for understanding human social cognition. *Neuroreport*, **18**, 467–71.
- Milgram, N. W., Adams, B., Callahan, H., Head, E., Mackay, B., Thirlwell, C. & Cotman, C. W.** 1999. Landmark discrimination learning in the dog. *Learning & Memory*, **6**, 54–61.
- Mitsui, S., Yamamoto, M., Nagasawa, M., Mogi, K., Kikusui, T., Ohtani, N. & Ohta, M.** 2011. Urinary oxytocin as a noninvasive biomarker of positive emotion in dogs. *Hormones and Behavior*, **60**, 239–43.
- Moll, H. & Tomasello, M.** 2007. Cooperation and human cognition: the Vygotskian intelligence hypothesis. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, **362**, 639–48.
- Molnár, C., Pongrácz, P. & Miklósi, Á.** 2010. Seeing with ears: Sightless humans’ perception of dog bark provides a test for structural rules in vocal communication. *Quarterly Journal of Experimental Psychology*, **63**, 1004–13.
- Morell, V.** 2009. Going to the dogs. *Science*, **325**, 1062–5.
- Mori, M.** 1970. The uncanny valley. *Energy*, **7**, 33–5.
- Morris, P., Fidler, M. & Costall, A.** 2000. Beyond anecdotes: An empirical study of “anthropomorphism.” *Society and Animals*, **8**, 151–65.
- Morris, P., Doe, C. & Godsell, E.** 2008. Secondary emotions in non-primate species? Behavioural reports and subjective claims by animal owners. *Cognition & Emotion*, **22**, 3–20.
- Morton, E. S.** 1977. On the occurrence and significance of motivation-structural rules in some bird and mammal sounds. *The American Naturalist*, **111**, 855–69.
- Mulcahy, N. J. & Hedge, V.** 2012. Are great apes tested with an object object-choice task? *Animal Behaviour*, **83**, 313–21.
- Munafò, M. R.** 2009. Reliability and replicability of genetic association studies. *Addiction*, **104**, 1439–40.
- Müller, C., Riemer, S., Rosam, C. M., Schöbwendler, J., Range, F. & Huber, L.** 2012. Brief owner absence does not induce negative judgement bias in pet dogs. *Animal Cognition*, **15**, 1031–5.
- Myowa-Yamakoshi, M.** 2003. Preference for human direct gaze in infant chimpanzees (*Pan troglodytes*). *Cognition*, **89**, 113–24.
- Nagasawa, M., Kawai, E., Mogi, K. & Kikusui, T.** 2013. Dogs show left facial lateralization upon reunion with their owners. *Behavioural Processes*, **98**, 112–6.
- Nakagaki, T., Yamada, H. & Tóth, A.** 2000. Maze-solving by an amoeboid organism. *Nature*, **407**, 470.

- Narita, M., Oyabu, A., Imura, Y., Kemada, N., Yokoyama, T., Tano, K., Uchida, A. & Narita, N.** 2010. Nonexploratory movement and behavioral alterations in a thalidomide or valproic acid-induced autism model rat. *Neuroscience Research*, **66**, 2–6.
- Nawroth, C., Ebersbach, M. & von Borell, E.** 2014. Juvenile domestic pigs (*Sus scrofa domestica*) use human-given cues in an object choice task. *Animal Cognition*, in press
- Neiworth, J. J., Steinmark, E., Basile, B. M., Wonders, R., Steely, F. & DeHart, C.** 2003. A test of object permanence in a new-world monkey species, cotton top tamarins (*Saguinus oedipus*). *Animal Cognition*, **6**, 27–37.
- Netto, W. J. & Planta, D. J. U.** 1997. Behavioural testing for aggression in the domestic dog. *Applied Animal Behaviour Science*, **52**, 243–63.
- Neumann, I. D., Maloumy, R., Beiderbeck, D. I., Lukas, M. & Landgraf, R.** 2013. Increased brain and plasma oxytocin after nasal and peripheral administration in rats and mice. *Psychoneuroendocrinology*, **38**, 1985–93.
- Nourbakhsh, I.** 1999. An affective mobile robot educator with a full-time job. *Artificial Intelligence*, **114**, 95–124.
- Odendaal, J.** 2003. Neurophysiological correlates of affiliative behaviour between humans and dogs. *The Veterinary Journal*, **165**, 296–301.
- Olazábal, D. E. & Young, L. J.** 2006. Oxytocin receptors in the nucleus accumbens facilitate “spontaneous” maternal behaviour in adult female prairie voles. *Neuroscience*, **141**, 559–68.
- Osthaus, B., Marlow, D. & Ducat, P.** 2010. Minding the gap: spatial perseveration error in dogs. *Animal Cognition*, **13**, 881–5.
- Overall, K. L.** 2000. Natural animal models of human psychiatric conditions: assessment of mechanism and validity. *Progress in Neuro-Psychopharmacology and Biological Psychiatry*, **24**, 727–76.
- Parker, H. G. & Ostrander, E. a.** 2005. Canine genomics and genetics: running with the pack. *PLoS Genetics*, **1**, e58.
- Parker, H. G., Shearin, A. L. & Ostrander, E. a.** 2010. Man’s best friend becomes biology’s best in show: genome analyses in the domestic dog. *Annual Review of Genetics*, **44**, 309–36.
- Passalacqua, C., Marshall-pescini, S., Barnard, S., Lakatos, G., Valsecchi, P. & Prato-Previde, E.** 2011. Human-directed gazing behaviour in puppies and adult dogs, *Canis lupus familiaris*. *Animal Behaviour*, **82**, 1043–50.
- Pepperberg, I. M., Willner, M. R. & Gravitz, L. B.** 1997. Development of Piagetian object permanence in a grey parrot (*Psittacus erithacus*). *Journal of Comparative Psychology*, **111**, 63–75.
- Piaget, J.** 1954. *The Construction of Reality in the Child*. Basic Books.
- Pineau, J.** 2003. Towards robotic assistants in nursing homes: Challenges and results. *Robotics and Autonomous Systems*, **42**, 271–81.
- Plutchik, R.** 2001. The nature of emotions. *American Scientist*, **89**, 344.
- Podos, J.** 1994. Early perspectives on the evolution of behavior: Charles Otis Whitman and Oskar Heinroth. *Ethology Ecology & Evolution*, **6**, 467–80.
- Pollok, B., Prior, H. & Gunturkun, O.** 2000. Development of object permanence in food-storing magpies (*Pica pica*). *Journal of Comparative Psychology*, **114**, 148–57.

Pongrácz, P., Molnár, C., Miklósi, Á. & Csányi, V. 2005. Human listeners are able to classify dog (*Canis familiaris*) barks recorded in different situations. *Journal of Comparative Psychology*, **119**, 136–44.

Pongrácz, P., Molnár, C. & Miklósi, Á. 2006. Acoustic parameters of dog barks carry emotional information for humans. *Applied Animal Behaviour Science*, **100**, 228–40.

Pongrácz, P., Molnár, C., Dóka, A. & Miklósi, Á. 2011. Do children understand man's best friend? Classification of dog barks by pre-adolescents and adults. *Applied Animal Behaviour Science*, **135**, 95–102.

Pongrácz, P., Hegedüs, D., Sanjurjo, B., Kővári, A. & Miklósi, Á. 2013. “We will work for you” – Social influence may suppress individual food preferences in a communicative situation in dogs. *Learning and Motivation*, **44**, 270–81.

Prato-Previde, E., Custance, D., Spiezio, C., Sabatini, F., Psicologia, I., Milano, U. & College, G. 2003. Is the dog–human relationship an attachment bond? An observational study using Ainsworth's strange situation. *Behaviour*, **140**, 225–54.

Price, E. O. 2002. *Animal Domestication and Behaviour*. CABI Publishing.

Quaranta, A., Siniscalchi, M. & Vallortigara, G. 2007. Asymmetric tail-wagging responses by dogs to different emotive stimuli. *Current Biology*, **17**, R199–R201.

Raab, A., Dantzer, R., Michaud, B., Mormede, P., Taghzouti, K., Simon, H. & Le Moal, M. 1986. Behavioural, physiological and immunological consequences of social status and aggression in chronically coexisting resident-intruder dyads of male rats. *Physiology & Behavior*, **36**, 223–8.

Range, F. & Huber, L. 2007. Attention in common marmosets: implications for social-learning experiments. *Animal Behaviour*, **73**, 1033–41.

Range, F., Horn, L., Virányi, Z. & Huber, L. 2009. The absence of reward induces inequity aversion in dogs. *Proceedings of the National Academy of Sciences of the United States of America*, **106**, 340–5.

Range, F., Leitner, K. & Virányi, Z. 2012. The influence of the relationship and motivation on inequity aversion in dogs. *Social Justice Research*, **25**, 170–94.

Rehn, T., Handlin, L., Uvnäs-Moberg, K. & Keeling, L. J. 2014. Dogs' endocrine and behavioural responses at reunion are affected by how the human initiates contact. *Physiology & Behavior*, **124**, 45–53.

Richard, S. & Zingg, H. 1990. The human oxytocin gene promoter is regulated by estrogens. *The Journal of Biological Chemistry*, **265**, 6098–103.

Richerson, P. J. & Boyd, R. 1998. The evolution of human ultra-sociality. In: *Indoctrinability, warfare and ideology: Evolutionary perspectives*, (Ed. by I. E. Eibesfeldt & F. K. Salter), pp. 1–24. Bergham Books.

Riedel, J., Schumann, K., Kaminski, J. & Tomasello, M. 2008. The early ontogeny of human-dog communication. *Animal Behaviour*, **75**, 1003–14.

Rimmele, U., Hediger, K., Heinrichs, M. & Klaver, P. 2009. Oxytocin makes a face in memory familiar. *The Journal of Neuroscience*, **29**, 38–42.

Rodrigues, S. M., Saslow, L. R., Garcia, N., John, O. P. & Keltner, D. 2009. Oxytocin receptor genetic variation relates to empathy and stress reactivity in humans. *Proceedings of the National Academy of Sciences of the United States of America*, **106**, 21437–41.

- Saldien, J., Goris, K., Vanderborght, B., Vanderfaellie, J. & Lefeber, D.** 2010. Expressing Emotions with the Social Robot Probo. *International Journal of Social Robotics*, **2**, 377–89.
- Saphire-Bernstein, S., Way, B. M., Kim, H. S., Sherman, D. K. & Taylor, S. E.** 2011. Oxytocin receptor gene (OXTR) is related to psychological resources. *Proceedings of the National Academy of Sciences*, **108**, 15118–22.
- Savage-Rumbaugh, E. S., Murphy, J., Sevcik, R. a, Brakke, K. E., Williams, S. L. & Rumbaugh, D. M.** 1993. Language comprehension in ape and child. *Monographs of the Society for Research in Child Development*, **58**, 1–222.
- Savaskan, E., Ehrhardt, R., Schulz, A., Walter, M. & Schächinger, H.** 2008. Post-learning intranasal oxytocin modulates human memory for facial identity. *Psychoneuroendocrinology*, **33**, 368–74.
- Scheele, D., Striepens, N., Güntürkün, O., Deuschländer, S., Maier, W., Kendrick, K. M. & Hurlemann, R.** 2012. Oxytocin modulates social distance between males and females. *The Journal of Neuroscience*, **32**, 16074–79.
- Scheier, M. F. & Carver, C. S.** 1985. Optimism, coping, and health: assessment and implications of generalized outcome expectancies. *Health Psychology*, **4**, 219–47.
- Scheier, M. F. & Carver, C. S.** 1987. Dispositional optimism and physical well-being: the influence of generalized outcome expectancies on health. *Journal of Personality*, **55**, 169–210.
- Scheier, M. F. & Carver, C. S.** 1992. Effects of optimism on psychological and physical well-being: Theoretical overview and empirical update. *Cognitive Therapy and Research*, **16**, 201–28.
- Scheumann, M. & Call, J.** 2004. The use of experimenter-given cues by South African fur seals (*Arctocephalus pusillus*). *Animal Cognition*, **7**, 224–30.
- Schuster, S., Wöhl, S., Griebisch, M., Klostermeier, I. & Wo, S.** 2006. Animal cognition: How archer fish learn to down rapidly moving targets. *Current Biology*, **16**, 378–83.
- Schwab, C. & Huber, L.** 2006. Obey or not obey? Dogs (*Canis familiaris*) behave differently in response to attentional states of their owners. *Journal of Comparative Psychology*, **120**, 169–75.
- Scollo, A., Gottardo, F., Contiero, B. & Edwards, S. A.** 2014. Does stocking density modify affective state in pigs as assessed by cognitive bias, behavioural and physiological parameters? *Applied Animal Behaviour Science*, in press
- Severinson-Eklundh, K., Green, A. & Hüttenrauch, H.** 2003. Social and collaborative aspects of interaction with a service robot. *Robotics and Autonomous Systems*, **42**, 223–34.
- Siniscalchi, M., Sasso, R., Pepe, A. M., Vallortigara, G. & Quaranta, A.** 2010. Dogs turn left to emotional stimuli. *Behavioural Brain Research*, **208**, 516–21.
- Siniscalchi, M., Lusito, R., Vallortigara, G. & Quaranta, A.** 2013. Seeing left- or right – asymmetric tail wagging produces different emotional responses in dogs. *Current Biology*, **23**, 2279–82.
- Skuse, D. H. & Gallagher, L.** 2009. Dopaminergic-neuropeptide interactions in the social brain. *Trends in Cognitive Sciences*, **13**, 27–35.
- Smith, L. B., Thelen, E., Titzer, R. & Mcllin, D.** 1999. Knowing in the context of acting: The task dynamics of the A-not-B error. *Psychological Review*, **106**, 235–60.

- Snowdon, C. T., Pieper, B. A., Boe, C. Y., Cronin, K. A., Kurian, A. V & Ziegler, T. E.** 2010. Variation in oxytocin is related to variation in affiliative behavior in monogamous, pairbonded tamarins. *Hormones and Behavior*, **58**, 614–8.
- Somppi, S., Törnqvist, H., Hänninen, L., Krause, C. & Vainio, O.** 2012. Dogs do look at images: eye tracking in canine cognition research. *Animal Cognition*, **15**, 163–74.
- Sophian, C. & Wellman, H. M.** 1983. Selective information use and perseveration in the search behavior of infants and young children. *Journal of Experimental Child Psychology*, **35**, 369–90.
- Soproni, K., Miklósi, Á., Topál, J. & Csányi, V.** 2002. Dogs' (*Canis familiaris*) responsiveness to human pointing gestures. *Journal of Comparative Psychology*, **116**, 27–34.
- Sosnowski, S., Bittermann, A., Kuhlentz, K. & Buss, M.** 2006. Design and Evaluation of Emotion-Display EDDIE. *2006 IEEE/RSJ International Conference on Intelligent Robots and Systems*, 3113–18.
- Stewart, A. M. & Kalueff, A. V.** 2014. Developing better and more valid animal models of brain disorders. *Behavioural Brain Research*, in press.
- Strunk, D. R., Lopez, H. & DeRubeis, R. J.** 2006. Depressive symptoms are associated with unrealistic negative predictions of future life events. *Behaviour Research and Therapy*, **44**, 861–82.
- Subiaul, F., Cantlon, J. F., Holloway, R. L. & Terrace, H. S.** 2004. Cognitive imitation in rhesus macaques. *Science*, **305**, 407–10.
- Sümeği, Z., Kis, A., Miklósi, Á. & Topál, J.** 2014. Why do adult dogs (*Canis familiaris*) commit the A-not-B search error? *Journal of Comparative Psychology*, **128**, 21–30.
- Syrdal, D. S., Koay, K. L., Gácsi, M., Walters, M. L. & Dautenhahn, K.** 2010. Video prototyping of dog-inspired non-verbal affective communication for an appearance constrained robot. In: *9th IEEE International Symposium on Robot and Human Interactive Communication*, Viareggio, Italy.
- Székely, T., Moore, A. J. & Komdeur, J. Eds.** 2010. *Social Behaviour. Genes, Ecology and Evolution*. Cambridge University Press.
- Taborsky, B. & Oliveira, R. F.** 2012. Social competence: an evolutionary approach. *Trends in Ecology & Evolution*, **27**, 679–88.
- Talbot, S., Freire, R. & Wassens, S.** 2014. Effect of captivity and management on behaviour of the domestic ferret (*Mustela putorius furo*). *Applied Animal Behaviour Science*, **151**, 94–101.
- Tami, G. & Gallagher, A.** 2009. Description of the behaviour of domestic dog (*Canis familiaris*) by experienced and inexperienced people. *Applied Animal Behaviour Science*, **120**, 159–69.
- Tardif, S., Harrison, M. & Simek, M.** 1993. Communal infant care in marmosets and tamarins. In: *Marmosets and tamarins: systematics, behaviour and ecology*, (Ed. by A. Rylands), pp. 220–234. Oxford: Oxford University Press.
- Taylor, K. & Mills, D.** 2006. The development and assessment of temperament tests for adult companion dogs. *Journal of Veterinary Behavior: Clinical Applications and Research*, **1**, 94–108.
- Téglás, E., Gergely, A., Kupán, K., Miklósi, Á. & Topál, J.** 2012. Dogs' gaze following is tuned to human communicative signals. *Current Biology*, **22**, 209–12.
- Theodoridou, A., Rowe, A. C., Penton-Voak, I. S. & Rogers, P. J.** 2009. Oxytocin and social perception: oxytocin increases perceived facial trustworthiness and attractiveness. *Hormones and Behavior*, **56**, 128–32.

- Thomson, A. P. D.** 1951. A history of the ferret. *Journal of the History of Medicine and Allied Sciences*, **6**, 471–80.
- Tomasello, M. & Kaminski, J.** 2009. Like infant, like dog. *Science*, **325**, 1213–4.
- Tomasello, M., Hare, B. & Fogleman, T.** 2001. The ontogeny of gaze following in chimpanzees, *Pan troglodytes*, and rhesus macaques, *Macaca mulatta*. *Animal Behaviour*, **61**, 335–43.
- Tomasello, M., Call, J. & Hare, B.** 2003. Chimpanzees versus humans: it's not that simple. *Trends in Cognitive Sciences*, **7**, 239–40.
- Tomasello, M., Carpenter, M., Call, J., Behne, T. & Moll, H.** 2005. Understanding and sharing intentions: the origins of cultural cognition. *The Behavioral and Brain Sciences*, **28**, 675–91.
- Topál, J., Miklósi, Á., Csányi, V. & Dóka, A.** 1998. Attachment behavior in dogs (*Canis familiaris*): A new application of Ainsworth's (1969) Strange Situation Test. *Journal of Comparative Psychology*, **112**, 219–29.
- Topál, J., Gacsi, M., Miklósi, Á., Virányi, Z., Kubinyi, E. & Csányi, V.** 2005. Attachment to humans: a comparative study on hand-reared wolves and differently socialized dog puppies. *Animal Behaviour*, **70**, 1367–75.
- Topál, J., Gergely, G., Miklósi, Á., Erdőhegyi, Á. & Csibra, G.** 2008. Infants' perseverative search errors are induced by pragmatic misinterpretation. *Science*, **321**, 1831–4.
- Topál, J., Miklósi, Á., Gácsi, M., Dóka, A., Pongrácz, P., Kubinyi, E., Virányi, Z. & Csányi, V.** 2009a. The dog as a model for understanding human social behavior. *Advances in the Study of Behavior*, **39**, 71–116.
- Topál, J., Gergely, G., Erdőhegyi, Á., Csibra, G., Miklósi, Á. & Mikló, M.** 2009b. Differential sensitivity to human communication in dogs, wolves, and human infants. *Science*, **325**, 1269–72.
- Topál, J., Miklósi, Á., Sümegei, Z. & Kis, A.** 2010. Response to comments on “Differential sensitivity to human communication in dogs, wolves, and human infants.” *Science*, **329**, 14d.
- Tóth, L., Gácsi, M., Miklósi, Á., Bogner, P. & Repa, I.** 2009. Awake dog brain magnetic resonance imaging. *Journal of Veterinary Behavior: Clinical Applications and Research*, **4**, 50.
- Törnqvist, H., Kujala, M., Somppi, S., Hanninen, L., Pastell, M., Krause, C. M., Kujala, J. & Vainio, O.** 2013. Visual event-related potentials of dogs: a non-invasive electroencephalography study. *Animal Cognition*, **16**, 973–82.
- Turcsán, B., Range, F., Virányi, Z., Miklósi, Á. & Kubinyi, E.** 2012. Birds of a feather flock together? Perceived personality matching in owner–dog dyads. *Applied Animal Behaviour Science*, **140**, 154–60.
- Udell, M. A. R. & Wynne, C. D. L.** 2011. Reevaluating canine perspective-taking behavior. *Learning & Behavior*, **39**, 318–23.
- Udell, M. A. R., Dorey, N. R. & Wynne, C. D. L.** 2008. Wolves outperform dogs in following human social cues. *Animal Behaviour*, **76**, 1767–73.
- Udell, M. A. R., Dorey, N. R. & Wynne, C. D. L.** 2010. What did domestication do to dogs? A new account of dogs' sensitivity to human actions. *Biological Reviews of the Cambridge Philosophical Society*, **85**, 327–45.
- Udell, M. A. R., Dorey, N. R. & Wynne, C. D. L.** 2011. Can your dog read your mind? Understanding the causes of canine perspective taking. *Learning & Behavior*, **39**, 289–302.

Van IJzendoorn, M. H. & Bakermans-Kranenburg, M. J. 2012. A sniff of trust: meta-analysis of the effects of intranasal oxytocin administration on face recognition, trust to in-group, and trust to out-group. *Psychoneuroendocrinology*, **37**, 438–43.

Vas, J., Topál, J., Gacsi, 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.

Vinke, C. M. & Schoemaker, N. J. 2012. The welfare of ferrets (*Mustela putorius furo* T). A review on the housing and management of pet ferrets. *Applied Animal Behaviour Science*, **139**, 155–68.

Virányi, Z., Gácsi, M., Kubinyi, E., Topál, J., Belényi, B., Ujfalussy, D. & Miklósi, Á. 2008. Comprehension of human pointing gestures in young human-reared wolves (*Canis lupus*) and dogs (*Canis familiaris*). *Animal Cognition*, **11**, 373–87.

Voelkl, B. & Huber, L. 2000. True imitation in marmosets. *Animal Behaviour*, **60**, 195–202.

Voelkl, B. & Huber, L. 2007. Imitation as faithful copying of a novel technique in marmoset monkeys. *PLoS ONE*, **2**, e611.

Voelkl, B., Schrauf, C., Huber, L., Oelkl, B. V & Uber, L. I. G. H. 2006. Social contact influences the response of infant marmosets towards novel food. *Animal Behaviour*, **72**, 365–72.

Waller, B. M., Bard, K. a, Vick, S.-J. & Smith Pasqualini, M. C. 2007. Perceived differences between chimpanzee (*Pan troglodytes*) and human (*Homo sapiens*) facial expressions are related to emotional interpretation. *Journal of Comparative Psychology*, **121**, 398–404.

Ward, A. J. W., Sumpter, D. J. T., Couzin, I. D., Hart, P. J. B. & Krause, J. 2008. Quorum decision-making facilitates information transfer in fish shoals. *Proceedings of the National Academy of Sciences of the United States of America*, **105**, 6948–53.

Werendich, D. & Huber, L. 2002. Social factors determine cooperation in marmosets. *Animal Behaviour*, **64**, 771–81.

Wilkinson, A. & Huber, L. 2012. Cold-blooded cognition: Reptilian cognitive abilities. In: *The Oxford Handbook of Comparative Evolutionary Psychology*, (Ed. by J. Vonk & T. K. Shackelfor), pp. 129–143. New Jersey: Oxford University Press.

Wilkinson, A., Mandl, I., Bugnyar, T. & Huber, L. 2010a. Gaze following in the red-footed tortoise (*Geochelone carbonaria*). *Animal Cognition*, **13**, 765–9.

Wilkinson, A., Kuenstner, K., Mueller, J. & Huber, L. 2010b. Social learning in a non-social reptile (*Geochelone carbonaria*). *Biology Letters*, **6**, 614–6.

William, W., Kahloon, M. & Fakhry, H. 2011. Oxytocin role in enhancing well-being: a literature review. *Journal of Affective Disorders*, **130**, 1–9.

Winslow, J. T., Hearn, E. F., Ferguson, J. N., Young, L. J., Matzuk, M. M. & Insel, T. R. 2000. Infant vocalization, adult aggression, and fear behavior of an oxytocin null mutant mouse. *Hormones and Behavior*, **37**, 145–55.

Yamasue, H., Yee, J. R., Hurlemann, R., Rilling, J. K., Chen, F. S., Meyer-Lindenberg, A. & Tost, H. 2012. Integrative approaches utilizing oxytocin to enhance prosocial behavior: from animal and human social behavior to autistic social dysfunction. *The Journal of Neuroscience*, **32**, 14109–17.

Yeates, J. W. & Main, D. C. J. 2008. Assessment of positive welfare: a review. *Veterinary Journal*, **175**, 293–300.

- Zak, P. J., Stanton, A. a & Ahmadi, S.** 2007. Oxytocin increases generosity in humans. *PLoS ONE*, **2**, e1128.
- Zentall, T. R.** 2006. Imitation: definitions, evidence, and mechanisms. *Animal Cognition*, **9**, 335–53.
- Zucca, P., Milos, N. & Vallortigara, G.** 2007. Piagetian object permanence and its development in Eurasian jays (*Garrulus glandarius*). *Animal Cognition*, **10**, 243–58.

Summary

The experiments included in this thesis present several different approaches of comparative social cognition research, all of which can be used to give various answers to the same broad question: “*in what is human behaviour special?*”. Although here the different approaches have been used to study different aspects of social cognition, the theoretical framework presented can be used to combine the methodologies and thus to study one specific question in an integrative way. From an evolutionary perspective it is interesting to study simple mechanisms that are potentially the basis of human socio-cognitive capacities. In order to do that we might investigate simple precursors of certain complex human behaviours in lower level vertebrates. Another approach investigates which of the human social skills are common with our phylogenically closest relatives and which are the ones that had been shaped by our special social environment and are thus similar to those of domestic species. Comparing human behaviour to that of primates, homologies in social skills can be identified suggesting a common evolutionary origin; alternatively uniquely human social skills might also be identified. The study of social behaviour in domestic species, and their wild relatives, can shed light to which skills have been formed by the human social environment resulting in behavioural analogies with potentially different underlying mechanisms. In order to investigate these mechanisms the genetic, neurohormonal or other physiological background of social behaviour needs to be studied. There is also an applied importance to comparative social cognition research. An example has been presented where humans’ understanding of the behaviour of an artificial agent was studied using simple behaviour patterns based on dogs’ social expressions.

Összefoglaló

A fent bemutatott vizsgálatok alapján elmondható, hogy számos különböző megközelítésmód alkalmazására van lehetőségünk a szociális kogníció komparatív vizsgálata során, amelyek mind más és más választ adhatnak ugyanarra a kérdésre: *“miben különleges az emberi viselkedés”*. Bár a disszertációban a különböző megközelítésmódok segítségével a szociális kogníció némiképp eltérő aspektusait vizsgáltuk, a bemutatott elméleti keret alkalmas lehet a módszertanok ötvözésére, és egy specifikus kérdés sokoldalú körüljárására is. Evolúciós szempontból érdekes a potenciálisan az emberi szocio-kognitív képességek alapjául szolgáló egyszerűbb mechanizmusok vizsgálata. Kérdéses például, hogy bizonyos komplex viselkedésmintázatok valamely egyszerűbb formája megjelenik-e alacsonyabbrendű gerincesekben is. Szintén láthattuk, hogy a filogenetikai megközelítésmódot a domesztikált állatok vizsgálatával kombinálva rávilágíthatunk, hogy az emberi faj mely képességei azok, amelyek közösek más főemlősökkel, melyek azok, amelyek az emberi környezetben élő fajokéhoz hasonlatosak, és melyek azok, amelyek humánspecifikusak. Azáltal, hogy az emberi viselkedést más főemlősökhöz hasonlítjuk olyan viselkedési homológiákon alapuló hasonlóságokat fedezhetünk fel, amelyek az adott tulajdonság evolúciós eredetére vezethetők vissza; ennek hiányában pedig speciálisan emberi tulajdonságokra világíthatunk rá. Az ember környezetében élő domesztikált fajok – illetve vadon élő rokonaik – vizsgálatával viselkedési analógiákat fedezhetünk fel, amelyek az azonos környezethez történő alkalmazkodás következtében jelentek meg; ezen analóg viselkedések bár funkciójukban azonosak, a mögöttes mechanizmus nagy mértékben eltérő lehet. Ezen mechanizmusok feltárásában segíthet a szociális viselkedések genetikai és neurohormonális hátterének illetve egyéb fiziológiai korrelátumainak vizsgálata. A szociális kogníció komparatív vizsgálata számos ponton kapcsolódik az alkalmazott tudományokhoz is. Például annak a kutatása, hogy különböző mesterséges ágensek által mutatott egyszerű viselkedésmintázatok miként érzékelnek az emberek, közelebb vihet minket ahhoz, hogy képesek legyünk a környezetünkben található ilyen ágensekkel szociális interakcióba lépni.