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

Thesis of Doctoral Dissertation

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## ***Introduction***

There is a common agreement that human social cognition can be considered special and that one of the key elements during human evolution was a change in social behaviour. Research aiming to unravel social skills that are uniquely human has identified several behavioural elements that differentiate us from other species. A crucial question in studying human social behaviour – as well as its biological background – in a comparative framework is what species to compare to. 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.

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.

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.

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.

This analogy-based approach has revealed that dogs (and possibly other 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). The combination these two lines of research could lead to novel research findings for example by the examination of 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.

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. 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). It has been suggested to view the human-robot interaction as an interspecific interaction and to use a non-human species, the dog, as a potential natural model for developing and testing social robots and human-robot interactions (see in detail: Miklósi & Gácsi 2012).

### ***General aims***

The aim of the present thesis is to combine different 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 taxon**

The present study used a bidirectional control procedure (Dawson & Foss 1965) to investigate whether a reptile species, the bearded dragon (*Pogona vitticeps*) is capable of imitating a conspecific. 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. In the two experimental groups the video-demonstration showed a conspecific approaching a sliding door, opening it rightwards

(or leftwards) and going through it. 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.

All experimental subjects successfully opened the sliding door whereas none of the control subjects did. Furthermore, on their first successful trial all experimental subjects opened the door to the side that they had observed the demonstrator opening. This side preference was consistent across the entire experiment with a significant 67-100% bias towards the demonstrated side. These results reveal *evidence of imitation similar to that described in birds and mammals in a reptile species (1. thesis)* and 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).

## **PART II: Phylogenetical approach**

This study takes a mechanistic approach to study the “A-not-B” error – a common object permanence phenomenon (Piaget, 1954) – in common marmosets (*Callithrix jacchus*). 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 – Csibra & Gergely 2006), and whether their success in the “B”-trials is influenced by the trajectory of the hiding of the target object. The experiment was carried out in the same way as in the infant study by (Topál et al. 2008). 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. 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. In the *non-social* condition, the E stood behind a curtain and hence the subject could not see her. 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.

Both “A” versus “B” trials and asymmetric versus symmetric tests had a significant effect on the subjects’ success while social versus non-social test situation had no significant effect. Both in the asymmetric and symmetric tests subjects performed above chance level in the “A” trials, but the number of successful trials in the “B” trials did not differ from the chance level. At the same time, subjects in the asymmetric “B” trials were less successful (made more

mistakes) than in the symmetric ones. 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 (2. thesis).*

### **PART III: Species adapted to the human environment**

#### **The domestic dog as a model of human behaviour**

In order to examine whether the attentional demands of a distractive component ('sham-baiting') of the hiding contributed to the dogs' "A-not-B" error in (Topál et al. 2009; 'Communicative-Hiding'), we tested whether dogs show a reduced tendency to commit the "A-not-B" error if location "A" is not sham-baited in the "B" trials ('Alleviated-B-trials'). Another argument, as often suggested in infant studies (e.g. Smith et al. 1999), is that subjects may commit the error in the "B" trials because they cannot inhibit the prepotent motor behaviour of searching at location "A" after doing so several times in the "A" trials. Thus, in a second group of dogs, by modifying the ostensive-communicative hiding procedure of (Topál et al. 2009), we examined whether dogs commit fewer errors if they only watch repeated hidings at location "A" but are not allowed to search there actively ('Watch-only-during-A-trials').

Dogs fetched the object reliably from behind screen "A" during the "A" 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 not only in the 'Communicative-Hiding' but also in the 'Alleviated-B-trials' and 'Watch-only-during-A-trials' groups. 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, leaving the Natural Pedagogy Hypothesis* (Csibra & Gergely 2006) *as the most probable explanation for the phenomena (3. thesis).*

#### **Another domestic species: ferrets**

In order to study a domestic species other than dogs we tested if in contrast to wild *Mustela*, domestic ferrets would 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.

In the Tolerance of eye-contact test we found that both domestic species looked more at their owners' than at the experimenter's eyes, while no such effect was found for the group of wild *Mustela* hybrids. In the Social-preference test both domestic ferrets and dogs chose their owners (as opposed to the experimenter) significantly more often than expected by random selection, while the wild *Mustela* hybrid group displayed a marginally significant preference for the unfamiliar experimenter. Finally, in the Responsiveness to human gestures test wild *Mustela* hybrids were less willing to participate than domestic ferrets both in the *Sustained touching* and the *Momentary pointing* task. Furthermore those subjects in the wild *Mustela* hybrid group that did complete all trials had a higher domestic ferret blood ratio than those that did not. Both domestic ferrets and dogs followed the human directional gestures above chance level in the *Sustained touching* and the *Momentary pointing* conditions. Wild *Mustela* hybrids however, did not succeed in any of these tasks. 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 certain types of human directional gestures (4. thesis).*

#### **PART IV: Biological background of dogs' social cognition**

##### ***Gene × behaviour associations***

Our aim in the current exploratory study was to search for preliminary evidence of possible associations between human-directed social behaviour and OXTR gene polymorphisms in two dog breeds (German Shepherds and Border Collies). The -212AG polymorphism was associated with Proximity seeking both in case of German Shepherds and Border Collies; carrying the G allele, was associated with lower proximity seeking in both breeds. The rs8679684 polymorphism was associated with Friendliness both in case of German Shepherds and Border Collies. 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. As a result of linkage disequilibrium the 19131AG polymorphism, similarly to the rs8679684 SNP, was associated with Friendliness both in case of German Shepherds and Border Collies. 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. This study provides the first evidence that *polymorphisms in the OXTR gene are related to human directed social behaviour in dogs (5. thesis)*.

#### ***The effect of intranasal oxytocin on behaviour***

In this study we investigated the effects of intranasally administered oxytocin (OT) on “optimistic” cognitive bias (Harding et al. 2004) in dogs. As previous research (e.g. Topál et al., 2009) 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. Dogs receiving OT pretreatment achieved a higher Positive Expectancy Score (“optimism”), than dogs receiving placebo (PL) pretreatment and this difference was more pronounced in the communicative context as reflected in a significant pretreatment × context interaction. There was no main effect of Com/NCom contexts. 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 and this effect is modulated by social task context (6. thesis)*.

#### **PART V: Dog as a model for social robotics**

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. Subjects readily attributed inner states to both the robot and the dog 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 and the robot. However, inner states were assigned more frequently to the dog than to the robot videos. Subjects were considerably successful when they could choose from the 5 possible emotional states. They could identify all dog, and all robot videos above chance level. However, subjects gave higher certainty ratings for the dog, compared to the robot videos. In sum, these results support the hypothesis that the dog is a promising animal model for integrating function and sociality to develop more “companion-like” social robots for different purposes, as *human observers are able to recognize emotions displayed by a robot by the means of behavioural patterns borrowed from dog behaviour (7. thesis)*.

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***Publications that form the basis of the thesis***

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