Big thoughts in small brains? Dogs as a model for understanding human social cognition

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In this review we argued that dogs can provide a good model for both the evolution of human social-cognitive abilities and studying the underlying neural and genetic structures of these behavioural features. The key difference between the present and other approaches for modelling human social evolution lies in the assumption that there is a large overlap between the human and dog behaviour complex because during their evolution in close contact with human groups dogs evolved functionally similar social skills. Thus the parallel investigation of the human and dog behaviour complex widens our possibility for understanding human social cognition because it allows the modelling of the interaction between various components in contrast to other models which are often restricted to modelling a single aspect of human social cognitive skills. *NeuroReport* 18:467–471 © 2007 Lippincott Williams & Wilkins.

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Introduction

After many years of neglect, dogs have made a real comeback in various fields of science, crowned by the publication of the dog genome [1]. It was preceded by increased interest among ethologists and comparative psychologists who advanced a very different view on dogs, especially by recognizing the significant role of the evolved dog–human relationship [2–4]. Novel behavioural methods and theoretical approaches allow the development of an alternative animal model which can revitalize many fields of science including cognitive ethology and genetics. Here, we will argue for a similar possible role in sociocognitive neuroscience.

Human analogue social skills in the dog

Together with others we have advanced the hypothesis that during the last 10 000 years of evolution dogs have developed a set of social skills that allow close integration with the human community. As a result, dogs became one of the most successful mammalian species. The human social environment selected for 'human-like' functional behavioural skills many of which have their analogues in humans. This provides a typical case for convergent evolution. It follows that dogs have the potential to offer an independent model for the evolution of social behaviour in contrast to other previously favoured organisms in which either practical methodological advantages (e.g. rodents) or close evolutionary homologue relationship (e.g. monkeys and apes) provided the scientific basis for comparative research.

The parallel between humans and dogs could become even more advantageous if one realizes that instead of assuming major dramatic alterations in social evolution of humans the process is viewed as a series of successive and parallel small changes in a wide set of social skills. Csányi [5] has proposed that these alterations affected sociality (e.g. life-long attachment, reduced intragroup aggression, enhanced cooperation), the ability to perform synchronized behaviour (e.g. imitation, hypnosis, dance) and complex constructive skills (e.g. mimesis, language). The set of the most important behavioural features that have undergone specific changes in our species has been summarized under the heading of the human behaviour complex. The success of present day *Homo sapiens* lies in the fact that it has accumulated a very efficient set of these abilities which led to the emergence of complex human-specific social skills.

The identification of sociocognitive skills in dogs could lead to a corresponding social behavioural model in the dog [dog behaviour complex (DBC)]. The overlapping elements of these behavioural complexes help to identify the minimum set of skills that had to be present at the beginning of *Homo* evolution. Research so far indicates that there is a substantial overlap among these behavioural complexes which widens our possibility for understanding human social cognition because it allows the modelling of the interaction between various components in contrast to other animal models which are often restricted to modelling only a single aspect of human social cognitive skills.

The complexity of the DBC revealed so far [2–4] suggests that human-like complex social behaviour and interaction at the group level is possible even in the absence of linguistic abilities. From the evolutionary point of view, this suggests

that early human groups could have engaged in cooperative interactions even if they did not possess the advantages of having a language. Thus, the DBC models an early stage of hominid evolution when people evolved a set of social skills that provided the basis for complex interaction. Social skills for attachment, rule following, the propensity for sharing information and social learning and imitation facilitated the manifestation of complex interactions at the group level [5]. Crucially, this analysis suggests that language was not a prerequisite for complex cooperative interactions in early humans.

Attachment and gestural communication

It is clear that the interspecific social behaviour of dogs has undergone major changes, which cannot be simply the result of environmental influences and must have some genetic basis. Recent research has just begun to identify many of these skills which involve various forms of heterospecific social learning (e.g. [6]) and cooperation [7]. Marked changes have been found in the vocalization (barking) pattern of dogs [8] in comparison to wolves, which very likely emerged in the course of the domestication process [9]. Next, we will highlight two particular aspects of social behaviour that have the potential to come in the focus of sociocognitive neuroscience.

In the psychological literature it is well known that humans develop an attachment relationship towards their dog [10], and it is also documented that young dog puppies show strong attraction towards humans. It has, however, turned out only lately that adult dogs live in an attachment relationship with their owner [11]. Using a method which was originally developed for testing attachment behaviour in human infants [12], we were able to show that a similar relationship is also present between dogs and their owners. In this so-called strange situation test (SST) the behaviour of the animal towards a familiar person (owner) and a stranger is compared, and observations have revealed a specific selective preference and responsiveness for the owner. Among other differences, for instance, we have found that, when left alone or when only the stranger was present, dogs ceased to play, and they showed more intense greeting behaviour towards their entering owner than to the stranger. More interestingly, this attachment behaviour developed quite rapidly in shelter dogs that were visited and interacted with for a short duration [13]. Before arguing for any species-specific changes in the dog, one should investigate whether the attachment behaviour is/was the result of the exposure to the social environment, or there are some dog-specific features involved. At present, two different observations are suggestive in this regard. Comparative investigations showed that, in contrast to dog puppies, hand reared, socialized wolf pups did not show a preference for the human caregiver over a dog, and in addition dogs showed more communicative signals (tail wagging, gazing) towards humans than the wolves [14]. In a subsequent SST we did not detect attachment-like behaviour in wolves [15], that is, they were not affected specifically by the absence of the caregiver and did not show selective responsiveness to her/him. Importantly, this does not provide evidence that wolves are not able to discriminate between humans. It shows, however, that, unlike dogs, for a wolf a human caregiver does not play a special, 'secure base' role in the case of a frightening and stressful situation. Newer research on dogs has indicated that frequent tactile contact is perhaps the most important factor for the development of the attachment relationship in comparison with food or other direct incentives [16]. Thus human-like attachment seems to be a species-specific feature in dogs which develops rapidly, can be expressed to various degrees towards many individuals of a group and is maintained life-long.

One critical condition of complex dog–human interaction is the effectiveness of interspecies communication. Recent experimental work has revealed that dogs have gone a long way in adapting to human communicative behaviour (see [4]). Although it was always thought that dogs are good at reading human gestures, experimental evidence was lacking. Recent research has provided evidence that dogs can use various forms of the human pointing gesture as a cue indicating the location of a piece of food (e.g. [18]). Dogs can also rely on novel, rarely used forms of the pointing gesture (e.g. cross-pointing or pointing with the leg [19]) and utilize arbitrary signals (e.g. putting an object near the hiding location [20]). Some researchers even assume that the dogs' performance in such tasks is superior to that of apes [2]. Dogs seem to be sensitive to the acoustic structure of a stimulus [21] and although verbal training is customary in dogs systematic investigations on this ability have started only recently. In contrast to dogs, hand-reared and socialized wolves cannot be trained to respond to verbal cuing. Only after extensive training would some individuals obey a sitting or lying command for a few seconds.

Importantly, dogs are also sensitive to human bodily signals that indicate attention. Recent research has uncovered that dogs are sensitive to direction of human gaze in very different contexts [22]. For example, dogs are less likely to be obedient (lying down) when the face of the commander is directed to another person or at an empty space. Similarly, when 'begging', dogs prefer to choose people who look at them [23], and have visible eyes. Although this latter effect is not very strong, comparative research suggest that dogs are more sensitive to eye/face-based human cues than chimpanzees [24].

Dogs also show specific behaviours as senders of signals when communicating with humans. Dog and wolf comparative investigations showed that dogs are superior in the initialization of communicative interactions. In one experimental situation, both dogs and hand-reared and socialized wolves were trained to solve a simple task by pulling a rope from under a fence to gain a piece of meat as a reward [25]. After both species had acquired this skill, we fastened the rope invisibly to the fence, thus pulling was not effective any more. In this situation dogs rapidly initiated a communicative interaction with their caretakers by looking at them whereas wolves continued to concentrate their efforts on getting the meat. Dogs also seemed to be able to direct the attention of their owner to the place of hidden food [26], or to a toy when 'it went missing' during joint play [27].

A perspective from neuroscience

Modern neuroscience has found diverse ways to tackle mechanisms underlying some basic sociocognitive behavioural skills. Although there might still be a preference for models based on a homologous argument other possibilities should also be considered. The decomposition of social skills by the behaviour complex approach described above allows direct comparison between elements of social skills

of humans and dogs. On the basis of these ideas, we illustrate this possibility by referring to the aforementioned behavioural forms of attachment and communication.

Social attachment

Psychological and neuropsychological research has always shown an interest in the neurobehavioural mechanism of formation (and malformation) of attachment behaviour. Recent research has developed a behavioural model which studies the underlying mechanisms by neurobiological and genetic methods (for a recent review, see [28]). Prairie voles (*Microtus ochrogaster*) are monogamous and live in lasting bonds; both parents provide extensive parental care, and even share their home with the young for some weeks after weaning. In contrast, montane voles (*M. montanus*) are promiscuous and do not form pairs and the offspring are abandoned early. Laboratory experiments have shown that this difference in pair bonding is mirrored in preference tests in which prairie voles show a clear preference towards their mate. A series of experiments has revealed that this species difference is paralleled by altered distribution of oxytocin and vasopressin receptors in some brain areas (e.g. prelimbic cortex, nucleus accumbens), in the sensitivity of these areas to external antagonists and agonists, and in the alteration of the promoter DNA sequence of the receptor gene. This suggests that small and well-defined changes at the neurogenetic level can lead to marked alteration in behaviour.

Although given the well-known conservative nature of the affiliative system (over the course of evolution), one can argue for a potential similarity between voles and humans, it might be worthwhile to investigate an 'intermediate' behavioural model provided by the dog. Above-mentioned behavioural evidence shows that the difference in affiliative behaviour displayed by socialized dogs and wolves towards humans is the result of the domestication process. Wolves are considered monogamous; the breeding male and female care together for subsequent generations of offspring that stay with the parents for 1–3 years. This suggests that the neuroendocrine basis of social behaviour in wolves could be organized along the same principles as that of the prairie vole. It follows that the functional similarity in the attachment systems of dogs has been achieved by special modifications of the system, some of which have a genetic component.

Moreover, evidence exists that selection for tame behaviour [29] exerts marked effects on the affiliative system in foxes, which show preference for interaction with humans. Although, for their brain, only changes in the serotonin levels have been reported [30] it is conceivable that selection affected other neurotransmitter systems.

Gestural communication

The finding that some neurons or neuron cell assemblies respond specifically to complex visual stimuli having significant social value has revolutionized the neuroscience of social cognition. Thus neurons in the temporal cortex of the macaque (*Macaca rhesus*) respond to systematically varied stimuli, such as faces with varied direction of gaze or body silhouettes varying in orientation [31].

More recently, the use of brain scanning techniques has verified the involvement of both temporal and frontal parts of the cortex in the processing of social cues in humans (e.g. [32]). Many studies have been aimed at finding out where and how the brain recognizes the state of attention based on a set of bodily and facial cues. Most authors seem to converge on the idea that the decoding of the significance of these stimuli takes place in at least three brain areas: the superior temporal sulcus, the amygdala and the orbitofrontal cortex. The main role of the amygdala is to evaluate the emotions associated with the face; superior temporal sulcus and orbitofrontal cortex are involved in the processing of particular facial cues such as head, mouth and eye motion [33,34].

The observation of a rapid head turn by a conspecific releases a seemingly automatic corresponding head turn towards the same direction in humans and in individuals of many other mammalian species. This reaction, referred to as gaze following [35], suggests that in many social species the rapid detection of the other's direction of attention confers certain advantages. Although in most cases gaze following might be an advantageous behaviour in competitive situations, cooperative interactions can also gain from the presence of such a skill. Interestingly, although chimpanzees are very skilful in gaze following, they utilize the advantages of this ability mainly in competitive situations [36]. Studies often report that apes do not perform well in social situations based on gestural signals (like pointing which also evokes gaze following) presented in a cooperative context [37]. It has been assumed that to perform well in cooperative situations subjects should go beyond simply representing the other's gazing direction but actually they have to achieve a state of attention sharing [35].

Although dogs show limited skills in following automatically the gaze orientation of humans into empty space [17], they are very sensitive to the direction of gaze and also to the presence of eyes. They are also very skilful in relying on gaze, head and pointing cues when they are given the possibility of searching for a hidden object [2,22]. Recent, comparative work has shown that the performance of dogs in such situations is comparable to children aged between 16 and 20 months (G. Lakatos, K. Soproni, A. Dóka, unpublished observation).

This ability might have some innate bias because dog puppies are superior in comparison to hand-raised and socialized wolf pups in such tasks [38]. Taken together, it seems that despite their divergent evolutionary history having evolved in a human-dominated environment dogs have adopted a set of communicative skills, which allow them to exchange information with humans. This raises the possibility that there are some shared brain mechanisms which are functioning in both dogs and humans.

Dogs in comparative biology

In the foregoing discussion, we have collected arguments to present the dog as a viable model for the evolution of human social cognition including the search for underlying neurogenetic mechanisms. Although certain parallels could have been drawn, and we believe in the plausibility of this approach, there are some issues for further debate.

One objection to our approach could be that 'dog-loving' scientists are prejudiced towards the dog and the performance of dogs in these experiments is the result of methodological sloppiness. In reality, however, most comparative behavioural tests have been adopted from ape and child research, and laboratories around the world have been

able to replicate each other's results. In fact this gives the real strength of this approach, because individuals of the same species are 'freely' available to ethologists or comparative psychologists working in any part of the world. If one assumes that sociocognitive investigations aim at revealing the skills of a natural population of humans, then to date the dog model is one of the main favourites in providing an experimental model.

The second objection tells us that the monkey–ape or even the mice–rat clade is more closely related to humans than the carnivores. Phylogenetically, carnivores are indeed more distantly related to men; however, even in the aforementioned clades homologies are also difficult to trace at the neural level. Moreover, recent comparative DNA investigations showed that in the case of many features the structure of the genetic material in dogs is more similar to that of humans in comparison to mice [1]. Thus, we argue that the mechanistic (neurogenetic) approach based on functionally analogous behavioural traits could provide an even more interesting insight into brain mechanisms, because dog–human convergence allows one to ask whether or how functionally similar performance in these species is controlled by partially or wholly different neural structure(s).

The third type of objection emphasizes that dogs' sophistication in their social competence is based on 'simple' learning resulting from extensive experience with humans. Although learning very likely plays a crucial role in the sociocognitive skills of dogs, the same argument applies also to apes or even human children. Moreover, among other experimental possibilities (which are not applicable in most primates) in the case of dogs we can also rely on a natural 'control' species, the wolf, to try to separate inherited and learned influences [2,38]. The marked behavioural difference between dogs and wolves exposed to the same human social environment suggests that learning mechanisms alone cannot provide an adequate explanation. In addition, dogs provide possible genetic variants ('breeds') which show marked differences in many features of social behaviour.

Future prospects for a noninvasive model

Dogs can be a model for an alternative neurobiological approach favouring exclusively modern noninvasive techniques of neuroscience. In general, all methods that are presently available and ethically applicable to humans can be utilized in freely living populations of dogs. Several such methods are available which if applied it simultaneously, could have a powerful effect. A starting neurogenetic approach could be based on the effects of allele polymorphisms on behaviour. For example, in the case of the dopamine DRD4 receptor an association with temperament-related behavioural traits has been described in humans [39]. Recent molecular genetic investigations revealed the presence of an analogue polymorphism in dog DRD4 receptor [40]. The implication of this polymorphism in human attachment [41] has potential for the elaboration of a dog model.

The noninvasive measurement of physiological parameters like heart rate variability or hormone levels (cortisol, testosterone) could also reveal psychophysiological changes paralleling sociocognitive behaviour. Investigations of this kind are already underway in the case of the dog–human relationship. In a preliminary study, we have also found that watching an emotionally valued object (ball) increases heart variability in dogs that like ball games (K. Maros, A. Dóka, Á. Mikósi, unpublished observation).

Finally, it has often been observed that in certain situations dogs express abnormal behaviours which show a close correspondence to human neuropsychiatric conditions. Reviewing extensive empirical data recently, Overall [42] has suggested that dogs could provide a natural model for certain human mental illnesses. Dogs proved to be also a useful model species for tracing mental changes in human ageing [43].

Conclusion

In this paper, we have argued that dogs can provide a good model for both the evolution of human social–cognitive abilities and studying the underlying neural and genetic structures of these behavioural features. The key difference between the present and other approaches for modelling human social evolution lies in the assumption that there is a large overlap between the human behaviour complex and DBC (see [4,5]) because dogs evolved functionally similar social skills. The critical step is to identify those elements of the behavioural complex that allow a meaningful comparison. Thus, the parallel investigation of the human and dog behaviour complex widens our possibility for understanding human social cognition because it allows the modelling of the interaction between various components in contrast to other models which are often restricted to modelling a single aspect of human social cognitive skills.

We also pointed out that recent advances in the study of the genetic and neuroendocrine basis of social behaviour could offer a new and fruitful approach for understanding the domestication of social cognition in the dog. Findings suggest that minor alterations in the regulating mechanisms could lead to comprehensive changes in sociocognitive functioning.

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