

Modelling behavioural evolution and cognition in canines: Some problematic issues

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Abstract Comparative behavioural research in canines may have the potential to add a new impetus for cognitive research on animals and humans. However this is a very young area that needs also re-thinking of old problems and questions which have been around for a long time. In this short essay we tackle three partially related problems: (1) interpretation of behavioural differences in dogs and wolves, (2) the idea of co-evolution of dogs and humans, and (3) issues of theory of mind.

We present a simple synergic model that takes both genetic and environmental factors into account in order to provide a balanced picture on the effect of domestication on dog behaviour, and how human social environment affects dog and wolf behaviour development. In the absence of evidence we argue against dog-human co-evolution in biological terms, leaving open the possibility for co-evolution at the cultural level. Finally, we suggest that the utilisation of complex cognitive models, such as theory of mind, is questionable, and actually more confusing in present day research on dogs' sociocognitive skills.

1. Introduction

The research on dogs has in many respects revitalised the field of comparative behavioural studies in general and the study of comparative cognition in particular. The rapid increase in the papers published on dogs' problem solving skills reflects clearly that in contrast to earlier scepticism showed by behavioural scientists toward dogs (see Udell et al., 2008) the study of this species has become fashionable. There are many theoretical and practical reasons why the study of dogs in a comparative framework seems to be a profitable endeavour. However, this approach is not without challenges. The fact that scientists from very different research

fields have been attracted by the topic in a short time, did not leave enough time for the emergence of commonly agreed research framework and methodology (see Miklósi, 2007; Udell, Dorey, and Wynne, 2010a). This applies also to theoretical approaches in case of which most of the disagreements stem from the mutual misunderstandings on how a particular concept, which originates from outside the present field, should be applied in the comparative studies of dogs.

Recently there have been various discussions on the role of "nature versus nurture" in three loosely interconnected research questions: (1) behavioural comparison of dogs and wolves (2) dog-human 'co-evolution', (3) 'theory of mind' in dogs. In this short review paper we avoid dwelling into the methodological details of experimental papers and the evaluation of those results because this has been done earlier in a much more detailed way (e.g. Miklósi and Soproni, 2006; Udell, Dorey, and Wynne, 2010a). In contrast, we aim to present some more general reflections

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on these issues by contrasting theories, exposing theoretical weaknesses and pointing out conceptual problems.

The picture is relatively uneven because some questions attracted more interest and thus more extensive data are available. This is especially true for the “nature versus nurture debate” that somehow got focused on the utilisation of human gestural cues in canines (Hare, Brown, Williamson, et al., 2002; Reid, 2009; Udell and Wynne, 2010b). In this particular case researchers invoked different types of models aiming to explain species-specific differences between wolves and dogs. In our discussion we try to push the debate toward a consensus by providing some additional insights that may have been overlooked earlier.

The notion on co-evolution of dogs and humans can be also found repeatedly in texts describing the history of dogs in relations to the anthropogenic environment (e.g. Reid, 2009). Unfortunately, many authors fail to provide any definition of the term, and the ideas with regard to co-evolution are used in a very vague way, without presenting much evidence for it. In this case our modest goal for the time being is to investigate in more detail whether the original evolutionary concept of co-evolution applies to the history of dog-human co-existence.

Finally, despite the fact that most research have been focusing on social problem solving skills in dogs, some of these problems have been re-formulated in the debated terms of “theory of mind” (e.g. Reid, 2009; Udell, Dorey, and Wynne, 2010a). Comparative research during the last 20 years (mostly in primates) have led to much discussion about the usefulness of applying this mental model to animals (see Povinelli and Vonk, 2003; Tomasello, Call, and Hare, 2003). The general impression has been rather negative partly because it was impossible to formulate clear hypotheses and researchers faced also many methodological obstacles (Heyes, 1993). Although it is not clear how such assumptions have infiltrated the dog literature after being found of not

much use in comparative research of primates, nevertheless we will try to make similar arguments for the canine case.

2. Contrasting hypotheses and working models on behavioural difference between wolves and dogs

The study of canine social problem-solving (for the explanation of using this term see below, 4.1.) behaviour has been in the focus of comparative behavioural research in the last 10 years (e.g. Bräuer, Kaminski, Riedel, et al., 2006; Miklósi, Kubinyi, Topál, et al., 2003; Pongrácz, Miklósi, Kubinyi, et al., 2001). Apart from an upsurge in experimentation, more or less detailed hypotheses have also emerged to explain behavioural differences within canines, with particular emphasis on dogs and wolves. Most researchers agree that today’s dogs and wolves share an ancestor in the past, and it follows that the divergent history of the two species should hold the key to understand why dogs and wolves live today in such different ecological and social environments.

It is however unfortunate that in parallel with collecting the behavioural data some researchers often missed to explain their behavioural models in detail, and others did not appreciate the role of these models in the scientific process. Moreover, the study of canines (as a “new” species in comparative behavioural research) seemed to have sparked very old debates on “nature-nurture” which have been outworn in other fields of ethology long ago. Two topics seem to be in the forefront of such discussions. The first concerns the evolutionary aspect of the emergence of dogs, including the process of domestication in the human niche. The second one is focusing on the nature of the canine mind or more specifically on the differences between the problem-solving ability (or “mind”) of the dog and the wolf. Note that these topics are closely interconnected because any difference in dogs’ and wolves’ problem-solving ability may originate in their divergent evolutionary past. Importantly, if we mention “difference in problem-solving

ability” then we refer to any difference in mental processing including acquisition, learning etc. (in sense Shettleworth, 2010).

Developing scientific models is just as important in trying to explain the observed phenomena as catalysing the thinking and work of the scientist. Further, these models aim to provide different type of explanations. Researchers often confound functional and mechanistic behavioural models. In our understanding functional models see behaviour as a means for survival. Such models of social problem solving predict the emergence of some well-defined behaviour skills (e.g. inter-specific social learning) and investigate how these may contribute to survival of the individual. In contrast, mechanistic models aim to explain social problem solving behaviour in terms of behavioural and/or mental mechanisms. It is important to note that the two types of models utilise different methodologies.

Take for example, the case of attachment behaviour that is suggested to provide the scaffolding of some social/communicational abilities. Topál, Gácsi, Miklósi, et al. (2005) have compared attachment toward the human caretaker in dogs and socialized wolves. They found that socialised wolves did not display most of the characteristic features of attachment behaviour which was present in the dogs. This finding has been used to suggest that attachment behaviour (see also Topál, Miklósi, Gácsi, et al., 2009), defined on the basis of behavioural criteria (e.g. Rajecki, Lamb, and Obmascher, 1978), was present in dogs but not in wolves. Udell, Dorey, and Wynne (2010a) criticised this study by noting that dogs have a longer sensitive period for socialisation with humans than wolves do. However, this criticism is truly missing the point of Topál’s conclusion. It has been well established that dogs need less amount of exposure to humans in comparison to wolves to reach similar levels of socialisation (e.g. Zimen, 1987). Topál et al.’ claim focused on the functional aspects of this skill, that is, attachment of dogs to humans may contribute to their survival in

the human niche. Our conclusion was based simply on the fact that subjects of both species received the same amount of socialisation before testing which was actually more than an “average” dog would receive. So the claim is that if wolves experience the same level of socialisation as dogs, they fail to show attachment toward their caretaker in that test. A mechanistic model of showing differences of attachment in dogs and wolves would need to involve a detailed and systematic comparison involving dogs and wolves of different ages and exposed to different amounts of human social experience.

At this point we would like to remind the reader that for a long time behavioural literature on wolves has served as a rich source of often very misleading anecdotes. For example, it was not until researchers did detailed observations on free-living wolves that we began to get a real insight into the social structure of wolves (e.g. Packard, 2003). The situation in comparative behavioural research on social problem solving is, however, more difficult because of the limited number of available wolves in captivity, and that even these differ in their genetic origin, developmental experience and experimental history. Unfortunately, this makes very difficult to design experiments that have the “resolution power” that is needed for mechanistic models. As we know from previous discussions (e.g. Hare, Rosati, Kaminski, et al., 2010; Udell and Wynne, 2010b), a large part of the mutual criticism refers to factors that were impossible to be controlled for properly because of the limitations of the experimental population. In such situation it is somewhat naive to assume that mechanistic modelling has the power to pinpoint at exact differences in mental mechanisms.

In the following we collect and contrast various hypotheses that aim to explain differences in dog and wolf behaviour with an emphasis on the confusing usage of functional and mechanistic arguments.

2.1 The so called “Domestication hypothesis”

The “domestication hypothesis” can probably be traced back to the paper by Hare, Brown, Williamson, et al. (2002) in which they interpret the dogs’ skilful utilisation of human gestures as being the outcome of the domestication process. They advance an “adaptive hypothesis” that *“it is likely that individual dogs that were able to use social cues to predict the behaviour of humans more flexibly than could their last common wolf ancestor ... were at a selective advantage”* (Hare, Brown, Williamson, et al., 2002). In another paper Miklósi, Kubinyi, Topál, et al. (2003) showed that dogs gaze faster at a human in comparison to wolves when they face an unsolvable situation. Those authors note that *“one of the first steps in the domestication of the dog was the selection for “human-like” communicative behaviours”* and add that *“the corresponding behaviour in dogs provides the foundation on which developmentally canalized complex communicative interactions can emerge between man and dog”*. Note that based on the above notions both experimental works aimed to develop functional behavioural models, and not mechanistic ones. This means that those authors did not specify any particular selective processes which may have acted on behaviour and they refer to the role of the developmental process in the emergence of these skills.

Thus it is somewhat misleading that in a recent paper Udell, Dorey, and Wynne (2010a) cite these two papers as example for what they call the “domestication hypothesis”. In their formulation *“the behavioural adaptations that make dogs a good fit for the human environment are a direct consequence of genetic changes that occur during domestication, independent of environment or life experience”*. It is the last part of this definition which is problematic because this interpretation does not follow from the logic of these (and many other) experiments and was never stated by the present author. Thus as such the “domestication hypothesis” was created by Udell, Dorey, and Wynne (2010a) themselves to expose an extreme position of genetic

determinism. It has been well-known for long (e.g. see Mason, 1968) that in the case of social mammals the developmental social environment plays an important role in shaping the social behaviour of the animals (see also Ginsburg, 1975 for the canine case). Nevertheless, if one refers to functional behavioural models, such social behaviours are regarded as being subjects of selective processes, despite the fact that at the individual level their full-blown development is environment-dependent.

Moreover, the reference to “domestication” assumes that this evolutionary process affected all species involved in the same way. Dogs have been domesticated much earlier than any other species, and have fulfilled different roles in the human environment, so species-specific targets of selection cannot be excluded.

Thus the “domestication hypothesis” as construed by Udell, Dorey, and Wynne (2010a) is clearly unrealistic and outdated, and its usefulness is questionable.

2.2 The “Two stage hypothesis”

Recently, Udell, Dorey, and Wynne (2010a) advanced a new hypothesis which they contrast with the “domestication hypothesis” described above. They place the main emphasis on two types of developmental experiences: (1) early interaction with humans during a sensitive period and (2) subsequent learning (about human behaviour in relation to “sought-after objects”) that is independent from developmental stage. Although the authors do not specify the mental mechanism underlying the first process, they refer to classical and operant conditioning in the case of the second type of experience. Additionally, they note that *“Unlike the Domestication Hypothesis of Hare & Tomasello (2005) and Miklósi et al. (2003), this alternative does not require the addition of a new mechanism, such as the evolution of human-like social cognition, during domestication.”*

It is clear that the “Two stage hypothesis” is providing a mechanistic explanation, which describes the observed behavioural outcome

in terms of well-known mental processes, as manifestations of associative learning. However, as exposed in the cited text above the authors did not say anything about the behavioural mechanisms that may account for the wolf-dog difference. The “human-likeness” of dogs with respect of some social skills has been used in a functional framework by Hare and Tomasello (2005) and Miklósi, Kubinyi, Topál, et al. (2003), as a behavioural analogy that is present in dogs, and not as a reference to a mechanism. It is an experimental matter whether and how dogs and wolves differ in their ability of utilising human pointing gestures (Miklósi and Soproni, 2006) but it is a fact that today many millions of dogs are capable of relying on such human signals, compared to those few wolves socialized specifically by enthusiastic scientists. Similarly, by assuming that dogs gaze preferentially at humans we do not refer to any mysterious “new mechanism” or “cognitive skill” (Miklósi, Kubinyi, Topál, et al., 2003). Some very simple genetic mechanisms could control for extended looking at “moving things with eyes”, a similar mechanism seems to account for preferential imprinting in chicks (Bolhuis, 1999). One difference is that when dogs or dog puppies look at human faces the human looks back for extended duration. This is important because it creates a very different developmental (learning) environment for the dog which may open up the possibility for further selective effects (see also Gácsi, Györi, Miklósi, et al., 2005).

Interestingly, Udell, Dorey, and Wynne (2010a) mention in passing that dogs may be “prepared” (in an evolutionary sense) “*to respond to stimuli displayed by social companions*” (p.338), and also acknowledge the possible role of lengthened ontogenetic window, and describe the possible differences between dogs and wolves as quantitative rather than qualitative. Unfortunately, these notions are used only as metaphors and lack any mechanistic explanatory power. For example, how can one decide whether a computer with a twice as big memory

capacity is quantitatively or qualitatively different from another one? It can certainly store more files (quantity) but it can also handle software with larger memory demand (quality).

It has been long assumed that domestication might have affected some kind of a sensitive period of these animals. Such an effect was observed in the foxes selected for tameness (Belyaev, Plyusnina, and Trut, 1985) in comparison to unselected companions. The former animals showed a developmentally delayed fear response to humans, and could be socialised during a longer period in comparison to unselected animals. Similar behavioural observations are available on dogs and wolves. Wolves can be socialised to humans only if the process is started very early (2-4 days of age) and is continued throughout the life of the animals (Klinghammer and Goodman, 1987). Although no qualitative comparisons are available a common interpretation of the present data suggests that dogs need much less social exposure to humans to achieve similar levels of socialisation than wolves (see also below).

The above mentioned experiment with the foxes selected for tameness may lead to a much less investigated question, namely, whether the selection resulted also in a specific preference for humans. Over generations foxes may have been selected for being attracted to the human odour, moving body parts etc. This genetic preference could be based on more generalised stimuli but had the power to potentiate and direct the development of behaviour during the sensitive phase. In the absence of direct experimental evidence one cannot exclude that changes in stimulus preference have also accompanied the lengthening of the sensitive phase in dogs. Preference toward the human face or some human odour could, in principle, have genetic underpinning. In similar vein Reid (2009) suggested also that such selective preference for human-based cues could have emerged as the result of specific foraging skills in dogs. Since their first contact with humans dogs were at

advantage if they figured out how human activities led to exploitable food sources.

The “Two stage hypothesis” seems to focus on two corresponding claims. It assumes that “*both domesticated and non-domesticated canids are equipped with the phylogenetic prerequisites to respond to human stimuli*” and as a consequence “*if a canid is adequately socialized to humans during its sensitive period of socialization and has experience with human behaviours that predict reinforcement ... then the individual should perform above chance on a related task whether or not it is genetically domesticated [sic]*”.

Unfortunately, it is not clear what the authors understand by “*phylogenetic prerequisites*” because one would have expected here a reference to behavioural mechanisms and not evolutionary terms. Similarly problematic is the reference to “*adequately socialized*” because it is clear that wolves need much more intensive socialisation than dogs. Thus Udell et al. see no difference between a dog socialised for a few hours per day and a wolf socialised for 24 hours per a day with humans, despite the fact that this species-specific difference must have genetic background and may influence also developmentally the final mental functioning.

The two-stage hypothesis is correctly emphasising the well-known role of the social environment in behavioural development but seems to throw out the baby with the bathwater by failing to acknowledge the role of selective factors on the behaviour which contributed to some species-specific behavioural differences between wolves and dogs. This approach is also problematic because the fundamental role of such comparative behavioural modelling is to explain species-specific differences and not, that certain environmental conditions may mask them.

2.3 The “Dog behaviour complex”

Let’s start with a note on function. The life of ancient humans cannot be compared with that of a present day dog breeder selecting animals for the possible tightest fit

to a conformation show standard. Our ancestors had little time and energy to invest in dogs (Morey, 2010). They only allowed those dogs to breed that were the best for whatever job they wanted them to do (or for no particular job at all) and they wanted dogs that could be maintained with as little effort as possible. Still one may argue that those ancient humans were “biophilic” (Wilson, 1984) and they may have shown anthropomorphic attitude toward animals (Serpell, 1996) by utilising human-specific social behaviours during interactions. Thus it seems reasonable to assume that they preferred those animals which were able to display mirroring social skills. The social behavioural correspondence between two individuals or the members of two species have been referred to as social competence (Topál, Miklósi, Gácsi, et al., 2009). Higher social competence leads to more complex social interactions either among conspecifics or among individuals of different species. We suppose that the evolutionary history of dogs in the human ecological and social niche enhanced their social competence which in turn allowed for the emergence of a range of different types of interactions, such as cooperation in herding (McConnell and Baylis, 1985) or guiding the blind (Naderi, Miklósi, Dóka, et al., 2001). We have stressed repeatedly that this approach is purely functional, that is, mutual social competence emerges at the level of behaviour and these outputs reflect very likely different mechanisms.

For example, Lakatos, Soproni, Dóka, et al. (2009) have shown that dogs and one and half years old children perform comparably when finding hidden food in a two choice task based on human pointing gestures. “Comparably” in this context means that there is no statistical difference between the number of food items found (“Performance”) in the case of most gesture types displayed by the human. However, it would be naive to suggest that this performance is controlled by the same mental mechanisms. Though somebody may argue that the social

environment and experience of a 1.5 years old child and a pet dog are similar, there are several differences as well. For example, the child is also immersed in an interactive linguistic environment and is developing such skills in parallel. Moreover, in contrast to the dog, the child has an arm and hand that is involved in object manipulation and communication, and such experience could be vital in relying on the communicative gesturing. It should be noted that emitting of gestural signals (sending) and relying on gestural signals (receiving) comprises to a single functional unit of behaviour, even if the two processes can be investigated independently, and in humans (for example), there is a developmental shift in the emergence of comprehension and production. From the survival perspective any human should be able to comprehend as well as produce these signals. This symmetry does not imply to dogs (just as apes in case of relying on linguistic signals) that leaves little room for arguments on mechanistic similarity.

Csányi (2000) introduced a descriptive evolutionary model that organised systematically those behavioural traits, which are either human-specific or were subjected to particular changes during the evolution of *Homo*. The significance of these behaviour traits is often acknowledged with different emphasis in the work of others, but the so-called "Human behaviour complex" stresses the mutuality and interdependence of these traits in making us humans. Rather than relying on a sequential account of human behavioural evolution (change in one skill enables the evolution of a different skill), this model visualises human evolution as a process of parallel changes with tight interaction (both genetically and developmentally) among these traits.

Broadening this approach Miklósi (2007) and Topál, Miklósi, Gácsi, et al. (2009) aimed to build a functional behaviour model based on notions originating from human behavioural evolution. Thus for the functional modelling of inter-specific aspects of social competence in dogs, it seemed to be useful

to introduce the idea of a "Dog behaviour complex". As in the human case, this complex contains those components of dogs' social competence for which there is behavioural evidence. In some cases the functional correspondence is relatively high, that is, there is a large behavioural overlap between the behavioural analogues of humans and dogs. Such relatively high correspondence has been described for attachment behaviour observed both in dogs (Topál, Miklósi, and Csányi, 1998) and humans (children) (Ainsworth, 1969). In other cases the human trait had to be decomposed to smaller units in order to reveal functional matching. Thus dogs may reach some levels in gestural communication as receivers but having no hands they present no match for humans as senders of such signals. Finally, there are obviously some human traits which do not have their functionally equivalent counterparts in dogs (e.g. musical skills).

In any case such comparative descriptive modelling of dogs' social skills in respect to human social skills is a useful way to decompose social competence into meaningful and testable units of behaviour. For example, this thinking led us to test whether dogs are able to show a functional equivalent of imitation behaviour (see Huber, Range, Voelkl, et al., 2009; Topál, Byrne, Miklósi, et al., 2006).

Thus any reference to "human-like social cognition" or "human-like social behaviour" should not be taken literally to suggest that dogs' mind is operated by mechanisms that are *on par* with respective human mental processing (see also below in relation with "theory of mind" arguments), instead such similarities reflect only functional correspondence.

2.4 The "Synergic model"

Gácsi, Györi, Virányi, et al. (2009) found that 4-month-old dog puppies seemed to show a better performance in the two-choice pointing task than intensively socialized wolf puppies of the same age. They discussed this finding in terms of interaction between

some genetic advantage on the part of the dog and its early social environment (see also Miklósi and Topál, 2011). This behavioural model has the advantage that it can be depicted graphically (see Figure 1), although both the independent measure (time) and dependent measure (inter-specific social skills) are arbitrary terms. The key feature of this model is that it recognises genetic differences between dogs and wolves which have the *potential* to lead to certain social competences in the human environment provided that certain environmental (social) conditions are met. The genetic makeup predicts separate developmental trajectories for wolves and dogs which, however, can be perturbed by the social environment. For simplicity the model recognises three levels of social input at the quantitative levels, and makes predictions for their effect in case of dogs and wolves. Importantly, the “Y” axis does not represent some “general social competence” but different behavioural skills, such as responsiveness to human gesturing, or attachment to humans. One may suppose that both the developmental dynamics (X-axis) and the social experience may vary with the specific behavioural trait.

There are two further aspects of this model that need consideration. First, we

assume that in order to be functional (in terms of survival) the social skill (or performance) should reach some threshold levels (Gácsi, Györi, Virányi, et al., 2009). For example, dogs have to perform over chance when relying on human pointing gestures. This level of competence is indicated by the dotted line. In practice such competence can vary within wide ranges, and has to be determined experimentally, separately for each social skill.

The second aspect relates to the levels of socialisation which may be regarded as arbitrary, but there is a general level of socialisation which applies to dogs living in or around human households. Given this premises the model gives a number of general predictions with regard to wolves and dogs. First, if both wolves and dogs are socialised in a way that is typical for dogs, the former do not reach the level of social competence that is acceptable in the human social niche for human-canine interaction. This could be either because dogs have some selective advantage over wolves in their early response to human cues (see Reid, 2009) and/or early differential developmental trajectory (see below).

Second, if exposed to intensive socialisation to humans wolves may reach the level

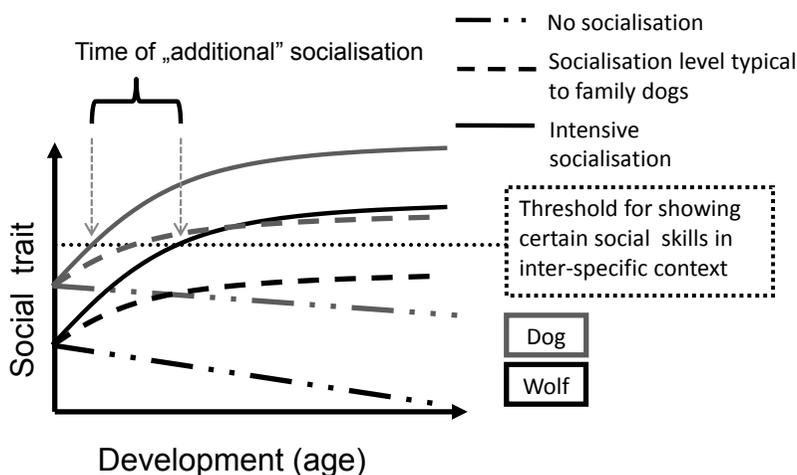


Figure 1. We present here an idealized model for comparing social competence in dogs and wolves, including the potential role of the social environment on the development of their social skills (see the text for details) (redrawn from Miklósi and Topál, 2011).

of acceptable social competence. This may be the case with wolves' utilisation of human pointing gestures. Importantly, however, due to the need for extensive socialisation wolves reach this level later in their ontogeny in comparison to dogs (Gácsi, Györi, Virányi, et al., 2009). Note that in the case of different social skills this developmental delay may vary based on the amount of additional socialisation needed and in some cases wolves may never pass this threshold of acceptable social competence. Based on our extensive experience with wolf behaviour, we may predict that even extensively socialized wolves would not show dog-like attachment toward their caretaker.

Third, by the nature of the developmental processes dog and wolf trajectories may cross each other that would reflect comparable inter-specific social behaviour or performance. Note however, that this only reflects a functional similarity and not necessarily similarity in the actual mental processes that control behaviour. Even if one supposes that the mind of a dog and a wolf may be operating in general according to the same principles, one cannot claim that the mind of a re-socialised stray dog and an extensively socialised wolf, that may actually show the same levels of social competence, actually relies on exactly the same mechanisms. This is because during their differential ontogeny these minds may have collected a different set of mental components for supporting the same behavioural outcome.

Fourth, the model also implies that the social environment plays a maintaining role in the social skills of both wolves and dogs. Despite being socialised to humans, these inter-specific skills deteriorate both in dogs and wolves in the absence of continuous human stimulation. However, the model claims a faster deterioration in wolves than dogs.

It may be worth to point out that there seems to be a fundamental difference in the intention of the modeller of the "two stage model" and the "synergic model". As noted above the former model places the emphasis

on the similarity while the later stresses differences in wolves and dogs. The time elapsed since the start of domestication of dogs at about 20,000-25,000 years ago resulted in genetic differences between dogs and wolves, which in both species reflect the selective effect on their respective environment. It seems also safe to assume that in the case of dogs the main selective force was the anthropogenic environment, and as a consequence dogs evolved to possess different morphological and behavioural traits. If one is aiming to explain such differences at the genetic level (e.g. Parker and Ostrander, 2005) then s/he needs to find well defined phenotypic traits. Thus behavioural research should have the important goal to pinpoint exactly that aspect of behaviour for which such genetic variation could be meaningful.

Such approach is also not without pitfalls. It is very important to understand the role of environmental factors in behaviour because one may easily draw erroneous conclusions if the effect of varying environmental influence is mistaken for genetic variation. This is why raising wolves and dogs in similar ways is important, although perfect similarity is difficult to achieve especially in case of adult animals. Testing of young individuals seems also to be important to reduce the divergent effect of the environment. Since a relatively large part of historic genetic variation in the wolf has been retained in the different dog breeds (vonHoldt, Pollinger, Lohmueller, et al., 2010), behavioural comparison of dog breeds rather than the wolves and dogs should lead to better behavioural models for genetic investigations.

2.5 The "Synergic model" and the argument on heterochrony

The development of dog morphology and behaviour is often discussed in the framework of phylogenetically induced shifts in development (e.g. Klingenberg, 1998). Heterochrony is an evolutionary concept that refers to the changes in developmental trajectories between an ancestor and a descendant species. In simple terms the organism may

pass fewer (paedomorphism) or more (peromorphism) developmental periods in relation to some point in distant time, which is usually the age at maturation. Accordingly, dogs develop slower in comparison to wolves because they retain some juvenile characters by their age of maturation. Thus dogs pass fewer developmental periods until they reach maturity. Although this concept has an appeal in a phylogenetic framework, it loses usefulness when explaining behaviour mechanisms. Researchers often refer to a species as being “paedomorphic” despite the fact that selective processes affect phenotypic traits and not necessarily the whole organism. A direct application of the hypothesis of paedomorphism to the morphology of dog skull faced also serious challenges (Coppinger and Coppinger, 2002) and seemed to be of little use in general. Instead of referring to paedomorphism or peromorphism affecting the whole organism in general, researchers should take a look at behavioural (or morphological) traits separately.

In contrast to general assumptions on paedomorphism in dogs, a detailed look at behavioural ontogeny in dogs shows that some traits develop in a similar pace to that of wolves, and some are actually emerging earlier in dogs than in wolves. For example, huskies start walking earlier than wolf puppies and retrievers, standard poodles, and huskies bark earlier than their wild relatives (Feddersen-Petersen, 2001; see Miklósi, 2007 for further discussion). These are clear cases for peromorphism that seem to contradict the general notion of the dog “being a paedomorphic species”.

It seems that Udell and Wynne (2011b) rely on this troubled notion of “paedomorphism” when criticising the synergic model. They disagree with our model because it suggests a faster development of inter-specific social skills in dogs in comparison to wolves. Note, however, that the synergic model actually relies on the finding that young dog puppies are superior to socialised wolves of the same age in utilising human pointing gestures on a two way choice task

(Gácsi, Györi, Virányi, et al., 2009). In other words dogs develop this social skill (achieve this performance) earlier than wolves. This may contradict the general notion of paedomorphism of dogs but it is in agreement with a more careful interpretation of developmental shifts as explained above. Actually, one could assume that peromorphism (earlier development) may emerge as the result of specific selection for a trait. For example, Feddersen-Petersen (2001) assumed that the early walking ability in huskies may indicate a selection for superior running performance. Thus such observations with regard to inter-specific social skills may reflect some selective advantage in the case of dogs in agreement with assumptions of Reid (2009) cited above. The fact that dogs show earlier development with regard to some human-oriented behaviour skills does not contradict those observations, which showed that other behavioural traits emerge later during dog ontogeny in comparison to the wolf.

The synergic model could also be seen as an expansion of the two stage model (see above and Udell, Dorey, and Wynne, 2010a) because it refers explicitly to both the genetic underpinning of developmental differences and reflects also on the dynamic interaction between phylogenetic differences and the nurturing environment. The synergic model could be applied also to other behavioural traits including aspects of intra-social behaviour or any other problem solving skill. Importantly, in this form the model does not make any predictions about the magnitude or direction of the developmental delay, level of competence or social experience. All these values should be determined experimentally which supply the input for the determination of developmental trajectories (see Figure 1).

3. Problems with the co-evolutionary argument

The implicit or explicit reference of dog-human relationship as being a case for co-evolution has a long tradition in texts about canines. One of the most detailed expositions was provided by Schleidt (1998) and a similar

argument using different type of evidence was presented by Paxton (2000). In contrast, most other notions of co-evolution do not enumerate any evidence, they simply take this situation as granted.

The simplest explanation for this situation is the literally translation of “co-evolution” as evolving “side by side” or being together on the same geographical spot. Importantly, however, co-evolution has a clear definition.

Evolution is often referred to as successive changes in allele frequencies (paralleled by phenotypic alterations) over long period of time as a response to environmental challenges. In similar vein co-evolution is implicated if one species exerts an important selective challenge on another which causes a specific evolutionary response by the second taxon, which in turn exerts a selective pressure on the first (e.g. Thompson, 1994), or more briefly, two or more species exerting reciprocal selection pressure on each other, leading to adaptation (Thompson, 1999).

One classic text book example concerns the co-evolutionary relationship between newts (*Taricha granulosa*) and garter snakes (*Thamnophis sirtalis*). Newts have evolved a powerful toxin (tetrodotoxins-TTX) that protects them from predators but the only major predator of this species evolved resistance to this poison. However, the poison of recent newts is actually much more powerful than what is necessary to kill a snake, so researchers assume that this reflects a case of co-evolutionary “arms-race” between prey and predator.

Thus any co-evolutionary scenario should involve at least one interaction between the two species that reflect mutual selective pressure. Using this logic Paxton (2000) argued that the superior olfactory ability of dogs may have relaxed selection for similar abilities in humans, which in turn allowed for anatomical changes that supported better speech skills. Schleidt (1998) has also argued that early humans may have learnt e.g. cooperative hunting or settling in a territory by observing wolves. Accordingly, present day humans may be the descendants of

those who showed interest in wolves’ behaviour and were the best to utilise such knowledge.

There are two critical aspects of any co-evolutionary theory. One must be able show that best explanation of the evolved trait(s) lies in the selective factor provided exclusively by the other species. The timing of the interaction is also important, that is, the selected co-evolutionary traits should emerge at the time when the selective environment is present, not before or after. It seems, however, that humans’ speech skills evolved before the time of dog domestication, and it is also likely that the social and hunting behaviour of humans (using tools and complex communication) had been quite elaborate before they encountered the wolves.

Thus in the absence of reliable evidence it seems that the textbook version of the co-evolutionary argument is not valid in the case of dogs and humans, and the co-habitation of dogs and humans affected only the dogs in terms of genetic change.

However, human-dog co-evolution may be still a viable concept if one extends the notion of evolution to human culture. Although there is a need to elaborate this concept in more detail, archaeologists and cultural anthropologists have accumulated a lot of data which suggest that dogs may have affected the evolution of early human culture. The presence of dogs in human communities may have lead to novel ways of exploiting resources, for example in the case of hunting or travelling over long distances. Such scenarios involved dogs with genetic changes affecting their morphology and behaviour but they probably did not affect human genetic constitution.

4. Cognition and mind reading: Do we know what we are looking for?

4.1 Cognition or problem-solving?

Sara J. Shettleworth, one of the most highly regarded comparative psychologists, defines cognition as collection of mechanisms by which animals acquire, store, modify information from the environment. In other

terms cognition involves perception, learning, memory and decision making (Shettleworth, 2010). Other prominent researchers prefer a more restricted definition, for example, they may discriminate cognitive from non-cognitive processes based on the type of information handled by the mind, while others refer to “lower” and “higher” type of processes.

In our view Shettleworth’s (2010) broad definition has an appeal for those working in the field of comparative cognition because its generality and descriptive nature. The reason for this is simple. When researchers conduct observations or experiments on mental phenomena in humans or non-human animals they collect behavioural data which represent usually a very crude (output) measure of the system (“mind”) studied. Logically, the model based on such data must be also a crude estimation of the mechanisms in the systems. This does not mean that such models of mental processes may not result in meaningful insights on how the mind may work in certain situations but researchers should be aware that present day methodology of comparative cognition is far from being realistic representation of the natural situation. Note that similar problems are present in other disciplines when researchers aim to replace *in vivo* experiments with *in vitro* methods. Clearly, most present day research on comparative cognition is an analogue to *in vitro* experiments (for similar arguments see Byrne and Bates, 2007).

The behavioural tally of “cognition” should be “problem-solving behaviour”, which is a much less fancy term, but at least reflects that the inference of any mental processes is made by using behavioural data. It is also clear that problem-solving is based on perceiving, learning, memory etc. but by describing this aspect of behaviour one can avoid the reference to “information” which is another problematic word. So we would prefer to (re-)define comparative cognition as a scientific inquiry that studies how perception, learning, memory and decision making controls problem-solving behaviour in animals and humans.

4.2 The unavoidable anthropocentrism of the “theory of mind” concept

Interestingly, the notion on the “theory of mind” was introduced in connection with the mental capacities of chimpanzees (Premack and Woodruff, 1978), but the idea made a real career in human developmental psychology (e.g. Perner, 1993). In most cases the skill of having a “theory of mind” is usually regarded as a synonym with the ability to attribute mental states to others, or in other words, having specific mental representations that in some way encode the hypothetical mental content of the other companion. The reference to ‘hypothetical’ is important because one has only indirect access to the others’ mental content. Adult humans may utilise the ability of mental attribution in two ways. For example, they may observe another to watching a dog, and make an inference that as a result of this exposure the watcher’s mind acquired a representation of the dog. Thus one may build a “second order” representation about the mental content of the other. However, in the lack of independent verification (e.g. asking: “Did you see this dog?”) one has no way to establish firmly that the particular mental representation actually has come to existence in the watchers’ mind, and will play a role in his/her future behaviour. Alternatively, humans may get involved in a social interaction by assuming that the other possesses certain mental representations. For example one may automatically assume that the mind of others contains information about a dog or dogs in general because he observed regularly people in the vicinity of dogs. Thus mental attribution is a mechanism that may build particular second order representation about the actual content of the others’ mind, and at the same time it may be a mental strategy that plays a causal role in initiation of behaviour in humans.

There is however an important point to add here. As noted above there are two ways for predicting the others’ behaviour. One may rely either on the supposed mental content of the other or on the behavioural cues

provided by the other. Now the question is which way of thinking provides the better or more reliable prediction. The subject may prefer to rely on behaviour cues (if present) because they may predict the behaviour of the other to a greater extent than relying in the supposed mental content. One may assume that utilising actual behavioural cues may be more efficient, and this would be the default choice. Subjects may switch to use mental attribution if there are no behavioural cues available, or the social situation is too complex for using simple behaviour-reading. Further aspect of mental attribution is that in order to utilise this skill there is a need for a much larger “data base” than for direct observation of behaviour.

One of the key aspects of mental attribution is that the mind should be able to represent intervening variables. For example, understanding of “seeing” (by the other) is such a variable or secondary representation. However, it is likely that the (human) mind is not born with such representation in place but has the basic skills to construct such representation(s) given the adequate environmental input. Thus mental representation of seeing emerges only after being exposed to hundreds of social situations in which the subject observes “seeing” by the others. Let’s take a statistical analogy! One may suppose that the mind is running a multivariate statistics similar to a factor analysis. Single behavioural variables (like being present, looking in that direction, obstructed gazing etc.) could serve as an input and the system aims at finding a common explanatory variable (“seeing”). Note that such explanatory (secondary) variables explain only a part of the variability present in the original (behavioural) variables and given the wide range of behavioural input variables, the explanatory power of the derived variable will depend on the size of the data base. Thus the subject’s mind will be able to derive a variable of “seeing” only if the computation rests on huge number of processed events. Note also that in the case of humans the linguistic environment provides

further support for this process, as the emerging derived variables (like “seeing”) can be strengthened by parallel linguistic verifications.

Thus it may be not surprising that mental attribution skills become more robust with increasing linguistic skills in human development, and any delay in collecting the required amount of experience (e.g. in children with hearing loss; Peterson and Siegal, 2000), leads to slower manifestation of this mental feature. Mental attribution in children can be easily verified in tasks depending on language while even adult humans are as likely to utilise simple behavioural cues displayed by the other as relying on mental attribution if the experimental tasks are presented in a non-linguistic context (Gagliardi, Kirkpatrick-Steger, Thomas, et al., 1995, see also below). This suggests that despite having robust mental attribution skills, humans tend also to fall back on behaviour reading if the situation offers such easy direct processing. In contrast, if the linguistic context of the social situation removes any observable behaviour cues then human subjects are forced to utilise mental attribution.

4.3 Testing “Theory of mind” in non-linguistic animals

Considering the above, it is not surprising that no convincing evidence for theory of mind exists in animals, partly because most experimental procedures introduce cues that can be used for behaviour reading, and partly because the much reductionist way of testing.

Consider for example the Knower-guesser paradigm, one popular experimental method for testing mental attribution in animals (Povinelli, Nelson, and Boysen, 1990; see also Heyes, 1993 for critical discussion). This procedure exposes the experimental subjects (chimpanzees) to two human partners (knower and guesser) of which only the knower is present and can witness when some valuable item (food) is hidden by a third person. Before the subject is allowed to make a

choice both partners indicate a potential location of the hidden item. The knower indicates the correct location while guesser indicates the wrong location. The mental attribution model assumes that the subject will base its decision on the assumed mental content of the partners (the witness had seen the hiding therefore he *knows* where the item is), alternatively a simpler behavioural interpretation would note that the subject will rely on the cues of the witness because he was present during the hiding. Importantly, successful performance on such trials does not reveal whether subjects are utilising mental attribution or behaviour reading.

In order to decide between these alternative explanations researchers add so-called transfer tests (Heyes, 1993) in which they manipulate the partners' chances to acquire information on the hiding. For example, in the original experiment both partners are present during the hiding but the guesser has a bucket over his head which prevents him from seeing. This test rests on the assumption that if the subjects are capable of mental attribution, they understand that buckets in this position prevent seeing, and consequently the acquisition of the hiding location. Thus subjects understand that seeing may lead to knowing. Importantly, the bucket over the head of the guesser represents also a cue. Subjects may simply learn during repeatedly testing that the partner with the bucket is an unreliable source of information. Accordingly, any claim about mental attribution can be made only if subjects perform correctly on the first occasion. However, there are actually many reasons why there is a high chance that subjects will eventually fail (like the chimpanzees did). From our previous discussion the most important aspect of this failure is that chimpanzees may have not collected any experience about the others' behaviour when they wear objects on their head. Although this notion may sound trivial but there is no evidence in humans that such experience is not necessary for the emergence of a similar skill in our species. One may argue that

chimpanzees may also cover their head and eyes occasionally by objects etc. but we do not know how much of such kind of experience is necessary to form the basis of a robust mental attribution skill (see above the analogy with factor analysis).

We may also note that the presence of a clear cue (bucket over the head versus no bucket) would have facilitated anyway the subject's thinking toward relying on behaviour reading. This is actually what happened when a similar experiment was performed with humans (Gagliardi, Kirkpatrick-Steger, Thomas, et al., 1995).

Although, Povinelli et al's experiment was also criticised on other grounds (e.g. chimpanzees may have difficulty in using mental attribution skills in cooperative situations, see also Hare, Call, Agnetta, et al., 2000), similar approaches to verify directly the presence of mental attribution skill in animals have lost their appeal. Most researchers have recognised that present day methodologies are too crude to provide insight into mental attribution in animals, and behavioural investigations should focus more on observable features of mental processing than hunting some elusive "cognitive ghosts".

4.4 Constructing a ghost of "theory of mind" for dogs

The theory of mind concept in the comparative behavioural research of canines seems to have emerged from nowhere, a bit similarly to the domestication hypothesis (see above). One location of its "birth" can be tracked down exactly. Reid (2009, p.326) writes that "*still others favour the suggestion that dogs' co-evolution with humans equipped them with the cognitive machinery to not only respond to human social cues but to understand our mental states; a so-called theory of mind (Miklósi et al., 2000, 2004).*" Unfortunately, this is a clear example of misquoting others' work because in those papers the authors did not mention that dog would utilise mental attribution during social interaction with humans. There is no refer-

ence to “theory of mind” and even the phrase “mental attribution” and “mental state” is not mentioned with regard to dogs. There is also no mention of “co-evolution” either.

In her review Reid (2009) acknowledges that there has been no evidence for mental attribution in dogs, and similar conclusion is made by Petter, Musolino, Roberts, et al. (2009). Thus it is surprising to see the idea re-emerging in Udell et al. (2011a) based on a problematic list of references. They implicate that dogs have displayed high level of performance in “*five out of seven theory-of-mind methodologies*”. This list, which is based on Heyes’ review (1998), is problematic for several reasons. First, most original authors of the cited papers did not claim that the dogs’ performance was based on mental attribution skills. Second, dogs in Petter, Musolino, Roberts, et al. (2009) actually failed the specific tests on theory of mind and the authors concluded that “*these experiments failed to provide any indication that dogs have theory of mind or understand the intentions of human testers.*” Further, it is difficult to see how the study by Miklósi, Polgárdi, Topál, et al. (2000) on ‘showing’ behaviour in the dog, was re-interpreted as being a case for “role-taking”. Finally, Heyes (1998) may have listed such experimental paradigms as having the potential to reveal mental attribution skills, research (including her own) during the last 10 years has shown many alternative ways of explanation. For example, Heyes (2001) does not assume that imitation requires mental attribution in humans.

Obviously, Reid (2009) and Udell et al. (2011a) may have reasons to predict the capacity of mental attribution in dogs but it is important to rely on appropriate references and indicate clearly if one re-interprets the results of experiments of other researchers. Interestingly in the discussion that followed the publication of Udell and Wynne (2011b), the original authors also admitted the uselessness of the “theory of mind” concept (“*perhaps it is time to acknowledge that the*

term theory of mind has outgrown its usefulness in comparative cognition studies”) and this was the main reason why we have been avoiding this concept altogether in our theoretical arguments in the last 15 years.

4.5 On the uselessness of “theory of mind” concept: Two examples

In a recent experiment Petter, Musolino, Roberts, et al. (2009) aimed to test whether dogs are able to detect human deception. Dogs were exposed to a somewhat modified version of the so called “deceptive pointing” experiment introduced by Woodruff and Premack (1979). In short, subjects are facing either a human (co-operator) who points always at the correct location of a hidden item (food) or another human (deceiver) who points always at the incorrect location. From the subject’s point of view the task is simple: it should choose the correct location based on the co-operator’s cueing and avoid choosing the cued location when facing the deceiver. As it has been pointed out earlier (e.g. Heyes, 1993) this experiment is problematic with regard to revealing anything about mental attribution because the way of presentation offers easy cues for behaviour reading for the subject. The task can be solved by recognising (learning) that in the presence of the co-operator one should choose the indicated location, and the non-indicated one should be chosen in the presence the deceiver. Thus there is no need to rely on any mental attribution, that is, subjects do not need to know that the deceiver has any intention of deceiving them.

As expected dogs chose the correct location in the presence of the co-operator but most interestingly, they failed to learn that they should choose the other (not indicated) container when facing the deceiver; they chose randomly (for a similar result see also Szetei, Miklósi, Topál, et al., 2003). Interestingly, their performance was better when the humans were replaced by black and white boxes. Based on these observations Petter et al. concluded that “*dogs are sensitive to the correlation between cues and their*

outcomes but offer no support for the idea that dogs understand human intentionality". Unfortunately, it has been never made clear what sort of evidence would have convinced the authors that dogs do understand humans' intention. It would be unrealistic to expect that dogs would recognise the deceiver is pointing to the wrong location on the second trial, but even if they had chosen the other location, they could have done this on the basis of inferring "deceptive intention" or rapid learning after a single exposure. However, either case is unlikely given the dogs' extensive exposure to "honest" humans all their life. The behavioural analysis revealed that during the deceiving trials dogs refused more often to approach any location, and they approached the deceiver human with longer latencies. This suggests that dogs were sensitive to the differences in the behavioural attitudes of the two experimenters, thus if dogs had been raised in a more deceptive social environment they might have performed better in this test. However, even in this case the experimental design would prevent one from arguing that the positive outcome supported exclusively the mental attribution explanation.

More recently Udell, Dorey, and Wynne (2011a) tested dogs (and wolves) in a begging task in which subjects had to figure out from whom it might be more profitable to beg for food (see also Gácsi, Miklósi, Varga, et al., 2004). Two experimenters were present at the same time, one of which had always visual contact with the dog (eyes uncovered) while the vision of the other was blocked in different ways (back turned, book in front of the eyes etc). Although the study could be criticised on methodological grounds (see Virányi and Range, 2011; Roberts and Macpherson 2011; Horowitz, 2011 but also Udell and Wynne, 2011b), here we are only interested in the researcher's attempt to reveal the "*possibility that successful canid subjects might also be able to infer the mental states of others.*"

This phrasing is rather surprising because, just as in the case of the previous

attempts, this experiment was also based on discriminating between behavioural cues of attention. Although dogs show some variation in responding to different cues (book, camera, bucket over the head) hiding the human's face, which may have an element of learning and experience, but this observation has little relevance with perspective taking. There is no need to take the perspective of the other if begging for food, simple behaviour reading makes the job just as well.

Reid (2009) argued also forcefully that dogs show strong scavenger attitude in the presence of humans. Thus the indiscriminate choice behaviour of shelter dogs in that experiment could also be explained by their strong motivation for feeding. In everyday situations dogs often receive food if they approach a non-attending human, so they are not inclined to utilise intervening mental representations in this task.

In a recent experiment dogs could observe that a human is hiding a piece of food at a location which was inaccessible to them (Lakatos, Gácsi, Topál, et al., 2012). Subsequently they were allowed to indicate this location in separate experimental trials either to a knowledgeable human, who was present during the hiding, or to a naive human, who had no knowledge about the location of the food. A purely logical interpretation of the mental attribution hypothesis would predict that dogs display more vigorous "showing" behaviour toward the naive human in comparison to the knowledgeable one. In contrast, we could not reveal such difference. Although this experiment did not aim for testing such hypotheses, in hindsight the behaviour of dogs indicates another type of logic. If it wants to get the food as fast as possible then the actual mental content of the helper is of less importance. Dogs indicated the location of food as vigorously as they could which was probably the best behavioural strategy in this case. In other words, this 'showing' behaviour in dogs has nothing to do with information providing but is rather an imperative behaviour that reflects the dogs' goal.

4.6 Looking ahead

Although some researchers may still entertain the possibility that dogs have mental attribution skills, but it seems that present day experimental methodologies are not able to provide robust evidence for such a claim. Moreover, as noted above it may be quite elusive to deduce complex mental phenomena on the basis of crude behavioural measures (such as making a choice between two options). Thus two different strategies may be useful.

Experiments should reflect more closely natural situations and more emphasis should be put on collecting detailed behavioural data. This approach would rely also on the introduction of new technologies that allow for gathering large amount of data without increasing the need for man power. Present day small scale laboratory testing may be optimal for collecting data but may not be adequate for investigating the problem at hand.

Alternatively, or in parallel, research should be centred at well-defined functional units of social behaviour and problem solving. Such a list of functional units is provided by the dog behaviour complex (Topál, Miklósi, Gácsi, et al., 2009), but there is room for different approaches. A behaviour-level analysis can provide a lot of insights in such functional phenomena as attachment, reconciliation, empathy without the need to explain them at the level of complex mental processes. We still know very little about the robustness and flexibility of these functional units, that is, to what degree these overlap with the corresponding human trait. It may be that on the whole social skills in dogs may represent a minimum level of social competence which is needed for being involved in meaningful social interaction with humans. The modelling of dog social competence may have far reaching consequences for understanding our own, and may pave the way for designing socially competent non-living agents as well.

Conclusions

Comparative cognition is a young discipline having a lot of potential, and this is even truer for such research conducted on canines. In the last century behavioural research on canines was often not taken seriously because dogs were seen as “artificial” animals which are useless in traditional, laboratory experiments. It has taken 15 years to change this trend, partly by re-defining the socio-ecological position of dogs, and putting the emergence of this species in an evolutionary framework that is tightly coupled with the modern history of humans. New laboratory approach has been developed that can accommodate testing large number of dogs worldwide. This comparative behavioural and cognitive research on dogs has a growing influence on the field. However, canine cognition should be featured as modern, inventive discipline and we should be able to avoid committing old mistakes, particularly those which have been outworn already by others.

Acknowledgement

This paper grew out of a short visit at Keio University for which I am extremely grateful to Professor Shigeru Watanabe and Dr. Eiichi Izawa. The topic selected for this discussion were chosen to reflect on those “burning” issues present in comparative cognitive research in dogs, and which help students to put both the theories and experimental work done by us and others in a critical perspective. During this time A.M. was also supported by Lirec FP7-ICT-2007. We are grateful to Márta Gácsi and Péter Pongrácz to provide comments to an earlier version of this manuscript.

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(2012. 1. 14 受稿, 2012. 6. 6 受理)