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What does it take to become 'best friends'? Evolutionary changes in canine social competence

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The traditional and relatively narrow-focused research on ape–human comparisons has recently been significantly extended by investigations of different clades of animals, including the domestic dog (*Canis familiaris*). Here, we provide a short overview of how the comparative investigation of canine social behaviour advances our understanding of the evolution of social skills and argue that a system-level approach to dog social cognition provides a broader view on the 'human-likeness' of canine social competence. We introduce the concept of evolutionary social competence as a collateral notion of developmental social competence. We argue that such an extended perspective on social competence provides a useful tool for conceptualising wolf–dog differences in socio-cognitive functioning, as well as for considering specific social skills not in isolation, but as a part of a system.

The comparative investigation of canine social behaviour

The interest in comparative social cognition originates from the quest to understand the evolution of human-specific skills or to collect evidence more generally for those selective factors that may promote changes in mental structures that control social functioning [1,2]. The traditional and relatively narrow-focused research on ape–human comparisons has been expanded by investigations of different clades of animals, including social insects [3], fishes [4], and birds [5]. In recent years, domestic dogs, 'man's best friends', have also attracted increasing attention from researchers interested in comparative social cognition. There has been a surge in both theoretical and experimental work, and the number of published papers has increased exponentially [6]. From a comparative perspective, dogs have become an interesting case, given increasing scientific agreement that their domestication can be considered as an evolutionary process [7], during which wolf-like capabilities were specifically transformed by the challenges of living with humans. Although the idea that some of the crucial components of human social skills can be found in dogs

offers an exciting possibility for comparative social cognition, there are heated debates in the literature and there is no scientific consensus on the validity of this approach. Thus, in the light of diverging views on canine social cognition, it may be useful to develop functional theories for systematising relevant research.

We review the available evidence and focus on those key social traits in dogs that are characteristic features of the functionally human-like nature of dogs' social competence. We will also provide a concise overview of the different theories that aim to explain the evolution of the canine mind and the role that domestication plays in the acquisition of socio-cognitive skills.

The comparative study of canine cognition offers a good opportunity to introduce the term evolutionary social competence (ESC – see Glossary). The advantage of this concept is that it provides a basis for a system-level view on mental processes and helps to integrate behavioural functions which until now have been studied in isolation. It also provides a useful concept for comparative investigations on the effects of proximate (developmental) and ultimate (evolutionary) determinants of canine socio-cognitive abilities in general and communication skills, in particular.

The functionally 'human-like' traits of dogs

Living in inter-specific groups with humans is one of the unique features of dogs. Based on this fact, various authors

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Glossary

Behavioural (phenotypic) plasticity: the potential capacity of a species to exhibit a range of (social) phenotypes in response to variations in the environment.

Developmental social competence (DSC): an individual's ability to generate social skills that conform to the expectations of others and the social rules of the group.

Enculturation: the socialisation processes through which an individual acquires the social rules and behaviour patterns of a human-centred environment.

Evolutionary social competence (ESC): an emergent property of interacting individuals that is manifested as a complex system of prosocial and coercive behaviour skills expressed by individuals of a species.

Set point: the set point of evolutionary social competence refers to a genetically determined default value of the system that determines the tendency to react in a coercive–prosocial way in social interactions.

Species-specific reaction norm: the degree of (social) behavioural plasticity of a species, which depends on its genetic endowment.

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(e.g., [8–10]) argue that it would be advantageous for dogs to display specific social skills for interaction with humans. It is often implicitly assumed that such social skills are functional matches of respective human traits, and thus are referred to as 'human (infant)-like' [8,11]. Indeed, research has uncovered a wide range of general, as well as more specific, social skills in dogs that seem to share important functional and behavioural aspects with those displayed by humans. A broader list of such traits is provided by Topál *et al*. [12]; here we focus on two illustrative examples.

There is evidence to suggest (e.g., [13,14]) that the relationship which develops between a dog and its owner fulfils the behavioural criteria of attachment (e.g., approaching the caregiver in times of emotional distress, using the caregiver as a secure base for exploration, etc.; see [15,16]). This is also supported by research showing characteristic features of attachment toward human caregivers in dogs, whereas wolves lack a similar behaviour-organising mechanism [17]. Advanced skills for attachment also ensures that dogs regard the human as a source of information [18], as well as protection and help [19].

More importantly, attachment has a fundamental role in the emergence of a complex system of inter-specific communication, because it allows the development of socially competent communicative interactions and synchronised collaborative activities between dogs and humans. A characteristic feature of human communicative interaction is that, in order to initialise and maintain communication, signals are often used in a specific ostensive–referential manner. Preverbal infants are able to profit from this highly interactive system (c.f. natural pedagogy [20]), because they show adequate responsiveness to the speaker's intention to communicate, as well as to those signals by which the speaker can specify the referent about which information exchange actually takes place [21].

Although dogs very likely utilise a different cognitive architecture for processing human communication than human beings, the shared, and 'demanding', social environment of dogs and infants raises the intriguing question of whether dogs demonstrate a somewhat infant-like receptivity to the ostensive–referential character of human behaviours. Ostensive signals, such as eye contact or directed speech (in a high pitched voice) serve not only to express the overt communicative intent of the human, but also to address the potential recipient. There is now increasing evidence that, in spite of their phylogenetic distance, dogs and human infants often show comparable performance at the behavioural level and dogs are able to fulfil some of the requirements of the receptive side of human communicative interactions [22].

Dogs, unlike wolves, show a positive affective response to human eye contact from early puppyhood onward [23] and they sensitively pick up human ostensive cues that may guide their attention in object search tasks [10,24–26]. More importantly, findings also suggest that dogs can comprehend the dual function of human ostensive signals. The establishment of mutual eye contact (e.g., in commanding situations) can act as strong addressing signals for dogs [27,28] and eye contact may also be an effective means of expressing human communicative intent [29].

These results support the notion that ostensive addressing, which can effectively form a ready-to-interact attitude in the dog, is an indispensable component of dog–human communicative interactions.

Another characteristic feature of canine–human communicative interactions is related to the referential character of human cueing. That is, in communicative interactions, humans often use signals with referential properties (e.g., pointing, gaze shifts, etc.). Ample evidence suggests that, like young infants, dogs rely on human directional signals that have potential referential significance [30,31]. They can utilise different forms of pointing gestures or gaze shifts to locate objects very flexibly [32], tend to relate to pointing as directional instruction [33,34], especially in a cooperative context [35], and are influenced by the directedness of some human emotional expressions [36]. Dogs are also willing to look at the human to obtain information about unfamiliar objects or events [18].

In addition, dogs seem to react to the information-transferring nature of communicative contexts in a specific manner: human ostensive–referential signals effectively activate a 'ready-to-obey' attitude in dogs [17,37] and, as a consequence, dogs show an increased tendency to act in line with the perceived instruction, without necessarily comprehending the causal structure of the collaborative interaction [38], even if the action is unusual or represents a counter-productive solution to the problem [10,26].

From a functional perspective, human-like aspects of attachment and communication allow the dog to engage in complex and complementing collaborative interactions with humans. However, despite the fairly general acceptance of the 'human-likeness' concept in dogs [8,12,25], several different hypotheses have been generated in order to account for the evolutionary causes of the specificity of canine social cognition and their behavioural and cognitive manifestations.

Comparison of theories that explain the emergence of 'human-like' social traits in dogs

Looking for hallmarks of dog inter-specific social skills in comparison to wolves has recently become a burgeoning field of comparative social cognition. Recent findings have prompted the scientific community to provide explanations to account for wolf and dog similarities or differences in socio-cognitive skills (see, e.g., [12,39–42]).

Although, most authors agree that during domestication humans provided the social environment which selected for dogs displaying human-competent social skills (e.g., [8,12,43]), there is ongoing debate regarding whether there is any substantive difference between dogs and wolves in the skills necessary for engaging in social interaction with humans (e.g., [11] vs [44]; [45] vs [46]; [47] vs [48]).

The so-called 'information-processing hypothesis' introduced by Frank [49] focused on the extreme plasticity and controllability of dog behaviour and proposed that wolves' species-specific social skills were complemented by more flexible cognitive processing. This gave rise to a single integrated system in dogs which enabled them to conform to the arbitrary nature of the human social environment.

Hare *et al*. [8], however, explained wolf–dog differences in terms of selection of communication-specific skills. The

idea that specific evolutionary changes might take place in the cognitive interpretive system is based on the hypothesis that dog communication skills reflect, at least to a certain degree, an evolutionary adaptation to the cognitively challenging human social environment, and, as a consequence, dogs have evolved functionally human-analogue social–communicative skills.

Inspired by the finding that selection of foxes for 'tameness' causes some correlated changes in a set of other behavioural and morphological traits [50,51], Hare and Tomasello [11] suggested that domestication affected mostly the aggression/fear response of the animals, which allowed their natural social cognitive skills to be expressed in the human environment. Accordingly, directional selection for tolerating the presence of human beings (specific evolutionary changes in emotional reactivity) was one of the most crucial factors in opening the door to the integration of dogs into human social groups. Importantly, this idea assumes that genetic changes affect mainly the less specific aspects of social behaviour.

More recently Topál *et al.* [12] utilised a system-theoretical approach and proposed that the domestication of social cognition in dogs is less likely to have occurred as a result of a fundamental change in one single aspect of the social–affiliative behaviour system. They claimed that canine social skills were fine-tuned by small genetic changes that affected different aspects (components) of sociality in concert (e.g., attachment, cooperation, increased social attention – see also below).

Others have emphasised the role of environmental influence and have favoured the position that much of the variation among dogs and wolves has a developmental (ontogenetic) origin. This view suggests that the evolutionary adaptation to the human environment is of negligible importance in the emergence of dog social communication skills. Thus, any specific genetic changes and/or changes in behaviour-organising mechanisms is neither necessary nor sufficient to account for 'human-like' social skills [42,52].

Although each scientific theory on the evolution of canine social cognition may have its merits, both methodological shortcomings in experimental research and the lack of a functional framework for social cognition have prevented the reconciliation of ideas emerging from the hypotheses above.

Genotypic and environmental variability in wolves and dogs and its role in comparative social cognition

Despite much effort to collect experimental evidence on canine social cognition, some already available insights in comparative research have not been taken seriously enough. It has been long recognised that comparison of behavioural skills (and cognitive mechanisms) is a difficult issue both theoretically and in practice [53,54]. Thus, it is very important that the methodology employed in experimental research should be as transparent as possible. For example, in order to investigate effects of the (social) environment on a species, one may compare similar genotypes (species) exposed to (living in) different environments or different genotypes (species) exposed to (living in) the same environment. Importantly, before such investigations can be carried out, one should collect data on the

possible (natural) variability in the genotypes and phenotypes, and also on the different kinds of natural (ecologically relevant) environments. Unfortunately, such in-depth analyses have not been carried out for the wolf and dog. Without aiming for a complete review of these issues, a few points are discussed.

Genetic variability is far from being uniform within wolves and dogs. Wolf populations, from which experimental animals may originate, are not only dispersed throughout the Northern Hemisphere, but some populations in East Asia, Europe and the Near East have been implicated to have played a substantial role in domestication, whereas others have not (e.g., wolves in North America [55]). In addition, there has been strong competition between recent humans and local wolf populations in Europe, but probably also in East Asia, which must have been selecting for avoidance of humans by wolves [55].

Even more complicated is the divergence of genetic variability in dogs [56]. Present-day dogs may be representatives of genetically isolated populations (breeds) or have a randomly mixed genetic background (e.g., mongrels). It is also likely that the former could have been under more stringent or more relaxed selection by humans (compare European and East Asian breeds), and populations of dog breeds suffer also from breed depression, founder effects [57], and more recently from the influences of local breeding regulations/preferences (working vs show types).

Similarly, both dogs and wolves experience quite different environments, especially in relation to contact with humans. Whereas for the wolf the lack of human contact characterises the ecologically typical situation, for dogs humans are an integral part of their typical environment. However, the dog–human relationship is very variable, ranging from the uncared 'village dogs' [58] to the highly respected family pet, which is treated like a child.

The role of the environment in shaping behavioural phenotypes has long been recognised in human and comparative psychology. It has also become apparent that environmental effects modulate the phenotypic expression of genotype (gene × environment interaction). However, the complex nature of such interactions in the case of the human social environment makes the experimental study of these issues difficult. For example, Tomasello and Call [59] have suggested that enculturated apes display socio–cognitive skills that exceed those exhibited by their wild relatives. Although it is not clear how epigenetically acquired social skills influence ape mentality [60], the same phenomena also play a role in the case of canines [12].

Unfortunately, many nuances of both genetic and phenotypic influences have been neglected when researchers theorise about canine socio-cognitive skills. Thus, there is a need to provide a broader framework in order to facilitate research and data collection.

Social competence: a central concept of comparative social cognition

The term social competence was first coined in developmental psychology [61] and has often been conceptualised as a developmental construct. This umbrella term is used to refer to skills that are essential for socially competent

functioning ('social skill-centred approach') or with regard to social outcomes that subjects achieve ('outcome-centred approach'). These traditional notions of social competence indicate an ability to generate 'appropriate' behaviour in specific social situations. 'Appropriate' in this context means that the individual conforms to the social rules and expectations of others [62].

Although the discussion above focuses on the developmental aspect of social competence (DSC), Stump *et al.* [63] have suggested a complementary, evolutionary approach. According to this view, individuals evolve social skills that allow them to control their resources (e.g., food, mates, information) within the social structure of the group. This suggests that the concept of social competence should be reformulated to include a wide range of both prosocial and coercive behaviours, which increase the fitness of the individual within its social group.

Recently, social competence in non-human species has been defined as the ability of an animal to optimise the expression of its social behaviour as a function of the available social information [64], acknowledging that the developmental environment may play a crucial role in determining this skill at the individual level [65].

Although behavioural (phenotypic) plasticity influences the range of behavioural skills displayed by an individual, it is also important to recognise that the degree of individual plasticity within a species may also depend on the genotype [66]. However, the evolutionary perspective on social competence suggests a step even further: major evolutionary processes (selective environment) that affect sociality could also cause changes in reaction norms of social behaviour at the species level [67]. Such species-specific reaction norms refer to the absolute degree of phenotypic plasticity, that is, the potential capacity of a species to exhibit a range of (social) phenotypes in response to variations in the environment. Thus, if one wishes to compare different species at the level of complex social skills, the introduction of evolutionary social competence (ESC) seems necessary. ESC can be defined as an emergent property of interacting individuals, which is manifested as a complex system of prosocial and coercive behaviour skills expressed by individuals of a species. Thus, in a comparative perspective we should focus on the species and not on the individual, and assume that species may differ (be constrained) in the degree to which they are able to react to challenges of the social environment.

Evolutionary social competence varies along a coercive–prosocial continuum and is determined by the past evolutionary forces which have optimised the species' behavioural system for specific functioning. Such forces include longevity, feeding behaviour, group size, and kin structure. This means that, despite the potential to develop a plastic phenotype, individuals of a species will show species-specific central tendencies.

One may hypothesise that a more prosocial ESC character has a stabilising effect on social interactions at the group level, allowing the species to organise in larger groups. Although relying on different social, mental and behavioural mechanisms, such a scenario was put forward for the evolution of humans (e.g. [20,68,69]).

Importantly, ESC has a profound influence on the relationship style among individuals in a group, including the organisation of cooperative actions and the management of conflicts. Flack and de Waal [70] defined a range of relationship types ('dominance styles'), from despotic through tolerant to egalitarian. In their framework, different monkey and ape species (including humans) are assigned to one category of these relationship types.

ESC provides a framework for understanding also why extensively encultured chimpanzees do not develop human-like social competence, despite their impressive behavioural plasticity [71]. The enculturation of chimpanzees has undisputedly a large effect on their social competence, but experimental observations also suggest marked differences if compared to humans [72]. Such constrains in ESC have often been referred to in the context of human–chimpanzee comparisons in terms of humans 'having a more cooperative nature'. Both theoretical arguments and experimental evidence have been presented for more competitive tendencies in chimpanzee social competence [72–74].

In our view, the introduction of a novel aspect of social competence may provide a useful unifying framework for incorporating both evolutionary (genetic) and developmental (experience-based) factors influencing social cognition. A further advantage of the social competence concept is that it models the social skills at a system level, in terms of relationships of functional modules that reflect specific aspects of the social interaction. Both features of the concept will be explicated using canine social competence as an example.

Inter-specific social competence in dogs

Theories of the emergence of canine social competence can be partly reconciled using the extended concept of social competence. Given that human ESC is biased for prosocial attitude (compared to other apes – see above), it is likely that a similar trend has prevailed in dogs (cf. social dog – causal ape [75]). In the course of domestication, human beings became an integral part of the dog social environment, which led to behavioural changes affecting ESC. This was probably a gradual process during which ancestral wolves with more human-like ESC tended to engage in closer social interactions with humans. Finally, humans also recognised the advantage of having a companion animal with some compatible social skills and increased the selection pressure on dog social behaviours (positive feedback) (see also Box 1). The result of this process was the emergence of an evolutionarily novel, inter-specific social competence in dogs, which allowed for the establishment of a wide range of social relationships with humans, ranging from a strictly working relationship to being a family pet [76]. It is likely that both parties have benefited from this inter-species relationship [77], which could be regarded as being mutualistic in nature.

Using the conceptual model of social competence (see also Box 2), we suggest that changes toward prosociality in dogs are reflected in (genetic) changes with regard to the set point of this system. This notion is most evident in Hare and Tomasello [11], who suggested selective effects on emotional reactivity with regard to aggression and fearfulness. Other theories [8,12,49] suggest both a shift in the set point and a genetic change that affects phenotypic plastic-

Box 1. Comparative methodology: ecological and developmental variations of the anthropogenic environment

From an ecological perspective, one may consider three main forms of human–animal relationship. Animals may exploit the resource-providing capacity of human communities (e.g., as a food source), but the animals' presence may also be harmful. Such inter-specific relationship is fairly competitive and humans often actively act against the intruding species. Rats *(Rattus norvegicus)* are good examples of such a competitive inter-specific relationship. Other forms are rather commensalistic (i.e., the intruder species benefits, whereas humans are unaffected), animals are tolerated in the community, and exceptionally, the relationship is also supported by humans (e.g., winter supply for urban birds). Finally, the human–animal relationship can also be mutualistic (both species benefit from the association) and the members of the non-human species are allowed to form intimate relationships with humans and are often treated like them. During their evolution, dogs (wolves) shared all these forms of symbiotic relationships with humans. The final stage of domestication was characterised by the emergence of a mutualistic relationship between humans and dogs, but, depending on the ecological and cultural situation, present-day dogs share all three forms of relationship with humans (Figure I) [40].

It is important to note that any socialisation process is an independent causal factor in the development of human–animal relationships. In experiments on comparative social cognition, relatively little care has been taken to expose dogs and wolves to similar environmental conditions. It is possible to identify three types of developmental environments. First, animals share their lives with conspecifics, but they are exposed regularly (and from early on) to human contact and interaction [49,83]. Second, wolves and dogs are raised (enculturated) as average family dogs, with relatively few specific experiences [84,85]. Third, animals are socialised in a specific way, by maximising the potential social effect [86], and specific methods are applied to prepare them for social interactions with humans [47,87].
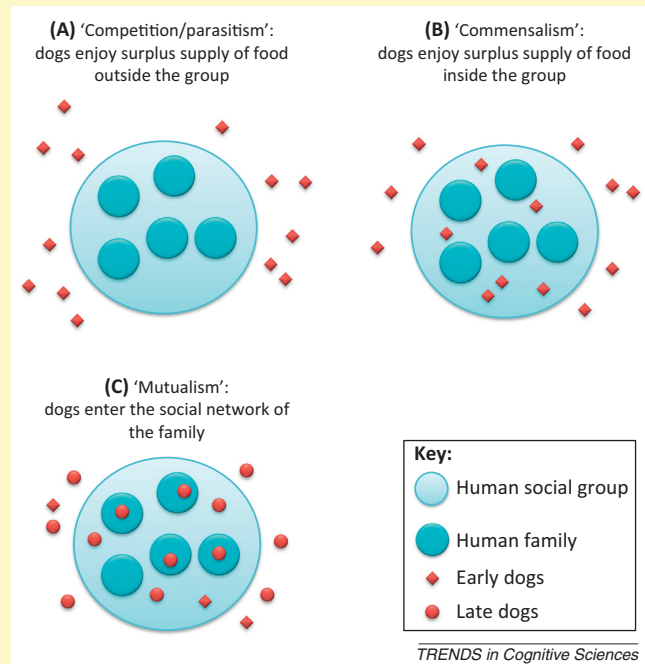

Figure I. Three different stages of dog-human interaction which are related to differences in social competence: **(A)** competition/parasitism; **(B)** commensalism; and **(C)** mutualism.

ity, that is, the magnitude of the species-specific reaction norm. In general it is assumed that dogs, compared to wolves, have a broader potential to adjust developmentally their social competence to the actual anthropogenic environment. The main difference between these latter concepts is that they hypothesise one [8,49] or many [12] set points in the system.

In contrast to these ideas, others [42] maintain that there has been no change in the set point(s) of social competence and only little if any change has emerged in the degree of plasticity of social competence during the domestication in dogs. Accordingly, most of the dog–wolf differences are related only to environmental (developmental) effects and can be compensated for by manipulating the anthropogenic environment.

We assume that (genetic) changes in the set point(s) and the degree (reaction norm) of behavioural (cognitive) plasticity must have induced a reorganisation of cognitive interpretive systems in the dog. As a consequence, dogs exhibit a different kind of socio-cognitive functioning in comparison to wolves. It also follows that the manipulation of the anthropogenic social environment is not sufficient to achieve dog-like social competence in wolves (see also Box 2). However, it is important to note that these issues can only be solved by careful experimentation (see above), and the actual effects may depend on the specific social skill involved.

Importantly, the intention behind the introduction of social competence is to facilitate thinking in terms of a self-contained system responsible for a diverse array of social functions which are manifested at the level of behaviour (e.g., co-acting/competing with others, sharing/not sharing

valuables, using/not using the other as a source of information). The outcome of these functions will determine the overall nature of social competence, which may be conceptualised along a one-dimensional scale (from coercive to prosocial). This view allows the identification of core and auxiliary modules/traits of social competence, the relationship among these modules, and the mode of functioning. It is important to note that this system-level approach does not necessarily reflect the cognitive mechanism that underlies behavioural control: functional analogies may be supported by diverse mental processes.

Accordingly, we assume that the core unit of dog social competence is their ability to form an attachment relationship with humans [78]. The significance of the dog capacity to form inter-specific attachment lies in the fact that, although in dog–human relationships there are no innate, pre-wired collaborative behavioural patterns (unlike in wolf–wolf interactions), this social skill serves as an organising background for the emergence of social competence in dogs. Further manifestations of dog social competence can be viewed as primary and secondary auxiliary modules that emerge and operate depending on the specific aspects of the human social environment. These modules are represented, for example, by complex communication skills, social learning abilities (including rudimentary forms of imitation [79,80]) and complementary cooperation [81].

Working with dogs could have been advantageous for humans frequently in their history and even today dogs are habitually employed by the police, army, and border patrol, help people with disabilities, or participate in various sports activities. The human-like social skills organised in a system of social competence provide the functional

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Box 2. Interpretation of comparative social competence in wolves and dogs

Figure I illustrates a theoretical relationship between evolutionary and developmental factors in wolves and dogs for the purpose of comparative analysis. We define three types of environments: living environments where humans are absent (Ea), living environments that provide typical human contact (e.g., family dogs, Etyp), and living environments that provide very high levels of human social contact with specific learning experience (specific socialisation experience, Es). The x-axis (horizontal axis) always refers to a specific (or complex) trait of inter-specific social competence, whereas the y-axis (vertical axis) refers to the number of individuals with a particular phenotype (i.e., the social trait under study).

We assume that the changes induced by domestication in ESC resulted in (i) a changed genetic set point (Sa: SPw⇨SPd) and (ii) a change in the species-specific reaction norm, that is, the capacity to react to the social environment (SRN1 and SRN2).

Accordingly, we assume that dogs display human-like social competence in the anthropogenic environment at a lower intensity of social stimulation than wolves (SRN1d > SRN1w). The quantitative relationship between SRN2d and SRN2w is uncertain, but wolves may have a greater potential here, mainly because of a ceiling effect in dogs. Note that the actual dog–wolf differences depend on the measures (traits) on the x-axis (horizontal axis).

We argue that, for comparative purposes, canine social competence should be related to the performance shown in a typical human social environment. Thus, maximum social competence (SCmax) is defined as the performance in a specific social environment (Es). This model suggests that SCmax will always be smaller (or equal) in the socialised wild species than in the evolutionary enculturated variant (Sa + SRN1d + SRN2d > SRN1w + SRN2w) and also provides a theoretical formulation of the selective advantage of domestication (SRN1d / SRN2d > SRN1w / SRN2w).

Obviously, however, SC represents a 'behaviour system' and therefore it cannot be tested directly. Instead, experimenters have to compare separate behavioural skills that are important in SC. In the past few years, researchers have accumulated much data on the performance of dogs when they relied on human pointing gestures in object finding tasks. Some of these results could be used as an illustrative example. The relatively poor performance of wolves in Hare et al. [8] could be ascribed to their lack of dog-like socialisation (Ea), because Miklósi et al. [9] and Virányi et al. [39] found comparable performance in dogs and wolves that had been socialised in the same way (Etyp). These observations were supported also by Udell et al. [41], who tested wolves socialised in specific ways (Es). Riedel et al. [45] found early development of this skill in dogs, supported also by comparative investigations on dogs and wolves by Gácsi et al. [84]. These studies suggest a shift in the developmental set point of this skill (see also [44]). In addition, genetic changes (affecting the set points) may be responsible for improved performance in dog breeds selected for wider heads or specific cooperative hunting skills [76,88,89].

Some predictions of the present model are also supported by earlier experimental observations. Socialised (Etyp or Es) wolves may perform as well as or even better than shelter (Ea) dogs [90,91]. At the individual level, some socialised wolves with specific social experience (Es) may exceed the performance of dogs living in Etyp or Es (see overlap between the distributions).
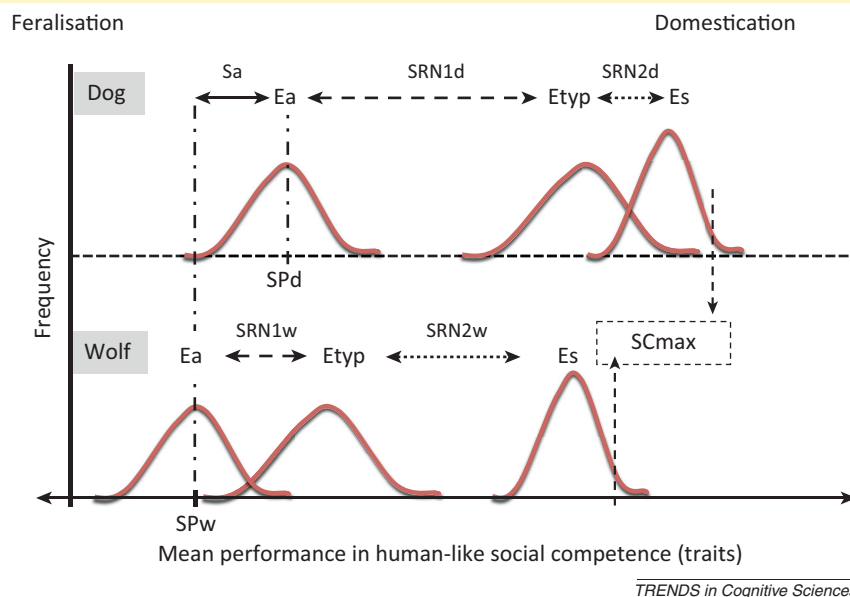

Figure I. A hypothetical model for comparing wolf and dog social competence with respect to evolutionary social competence and species-specific reaction norms.

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basis for deploying dogs as working partners that replace humans, especially as dogs seem to have a tendency to improve their performance, a functional analogy to human expertise [82].

Concluding remarks

Recent research on canine social cognition has provided a rich experimental basis for inter-specific social skills in dogs that live in the anthropogenic social environment. Although some fundamental differences exist among theories that explain the emergence of these skills, it should be noted that in the light of present evidence none of them can be refuted. It is easy to acknowledge that, in the absence of strict experimental control for genetic and environmental factors, any differences (or similarities) between wolves and dogs have to be viewed critically, especially in the case of evolutionary arguments. It may be added that there is also a difference in research agendas. Whereas some researchers aim to determine how environmental modifications could give rise to 'maximum' performance with regard to hetero-specific social competence, others are more interested in how the natural (anthropogenic) environment of dogs (which is characterised by the selective factors of domestication) affects their socio-cognitive skills. Although recent research provides an unprecedented opportunity to expand our

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Box 3. Questions for future research

- Comparative research in dogs and human infants raises the question of whether we can identify basic similarities and differences in the organisation of species-specific social competence at the levels of both behaviour and cognitive functioning. This question could be operationalized by introducing non-invasive methods, for example, eye-tracking technology (e.g., [29]), brain imaging (e.g., [92]), and candidate gene analysis (e.g., [93]).
- In order to gain deeper insight into the socio-cognitive functioning of dogs, we also need to explore the neurochemical and neuroanatomical factors of social competence. In light of recent human studies, it would be important to know what role endogenous oxytocin plays in modulating dogs' susceptibility to human ostensive communicative signals.
- There is evidence that preverbal infants' responsiveness to human ostensive referential signals has its parallels in the behaviour of dogs (e.g., [29]). It is unclear, however, whether there are some dog breeds that are innately better prepared to become proficient in using human cues of communication in an infant-like manner (e.g., [76]).
- How can the concept of dog social competence transform applied aspects of dog behaviour, such as dog training? For example, a more deliberate utilisation of social learning in dog training may improve dogs' performance.

knowledge of canine social cognition, the field is still in need of those carefully controlled comparative experiments that could uncover the cognitive mechanisms controlling social competence. Undoubtedly, all this could be in vain if researchers do not develop clear-cut guidelines for dealing with effects of the genotype and high environmental variation. This work could be facilitated by examining other levels of biological organisation, for instance, by investigating comparatively the neural and genetic control of behaviour.

In summary, dogs and humans do not only share prosocial qualities of social competence, but some components of the social competence of dogs can be considered as functioning in the same way as those in humans. This similarity makes dog social competence appear sometimes 'infant-like' or 'human-like', but, importantly, the underlying mental mechanisms may turn out to be quite different (Box 3).

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