Evolutionary approach to communication between humans and dogs

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Summary. Dog-human communication has been widely investigated recently for different theoretical reasons, in most cases through dogs' comprehension of human gestural cues. Dogs have been reported to be very skilful in comprehending a variety of human pointing gestures in many independent studies. This paper provides a short overview of the possible explanations behind the dogs' exceptional communicational abilities towards humans from an evolutionary perspective, concluding that the different and seemingly contradictory hypotheses are not exclusive but they might have a synergic effect.

Key words: dogs, communication, pointing, domestication, socialization.

Riassunto (Approccio evoluzionistico alla comunicazione tra cani e uomini). La comunicazione tra cani e uomini è stata oggetto di numerosi recenti studi, soprattutto indirizzati all'analisi della capacità dei cani di comprendere segnali gestuali umani. In numerosi studi i cani hanno dimostrato elevate abilità nella comprensione di una varietà di gesti umani aventi lo scopo di indicare. Questo articolo rappresenta una breve rassegna dei possibili meccanismi alla base dell'eccezionale capacità dei cani di stabilire un sistema comunicativo con l'uomo. A tal proposito, le diverse ipotesi, apparentemente contraddittorie, potrebbero non escludersi vicendevolmente e i meccanismi coinvolti potrebbero aver avuto un effetto sinergico sull'emergenza di tale abilità.

Parole chiave: cani, comunicazione, indicare, domesticazione, socializzazione.

INTRODUCTION

Dog-human communication received increased interest lately in ethology and has been investigated for different theoretical reasons. The most commonly used method for investigating dog-human communication is examining dogs' capacities to utilize human gestural cues, like pointing.

The pointing gesture is a human-specific signal, which is referential in its nature. It is a foundational building block of human communication and omnipresent in our everyday interactions [1]. The fact that the pointing gesture is one of the communicational tools that human infants acquire most rapidly, weeks before the first spoken word, also emphasize its importance in human communication [2].

In humans the pointing gesture can take many forms in everyday life. Although in most cases we point with the extended arm and index finger ipsilateral to the objects, variations in the position of the upper arm and the hand with respect to the body can be observed.

To investigate the evolutionary roots of the comprehension of this human-specific gesture, different evolutionary approaches have been considered based on either divergent or convergent evolutionary processes.

EVOLUTIONARY MODEL BASED ON DIVERGENT EVOLUTIONARY PROCESSES

This evolutionary approach is based on the observation that the pointing gesture is a uniquely human behaviour that emerges only in our species under natural circumstances [3]. Collecting experimental evidence for such human distinctiveness requires comparative data on humans and related primate species. Differences and similarities could shed light on whether abilities to comprehend pointing gestures are restricted to humans or have some evolutionary antecedents [4].

For this reason many different primate species have been tested for pointing comprehension, like rhesus monkeys (*Macaca mulatta*), capuchin monkeys (*Cebus apella*), chimpanzees (*Pan troglodytes*), gorillas (*Gorilla gorilla*), orangutans (*Pongo pygmaeus*).

EVOLUTIONARY MODEL BASED ON CONVERGENT EVOLUTIONARY PROCESSES

A different line of argument suggests that convergent evolutionary processes could also lead to the emergence of such abilities. Similar environmental effects and selection pressures could also produce appropriate conditions for the emergence of such communicational abilities just like common evolutionary history and divergent evolutionary processes.

For this reason it was suggested that the dog could be a suitable model species for studying early human evolution as well. In the course of the domestication in parallel to earlier human evolution many different abilities have been evolved in dogs, which are analogues with the elements of the human specific behaviour-complex. It is important to note that in this model one can talk only about functional similarities in the behaviour and it is unclear if there are similar mechanisms behind these abilities in the case of humans and dogs.

COMPREHENSION OF HUMAN COMMUNICATIVE SIGNALS IN DOGS

Dogs have been reported to be very skilful in comprehending a variety of human pointing gestures in many independent studies [5-9].

Dogs were found to be able to choose on the basis of both proximal and distal pointing gestures and the same is true if we look at the staticness of the pointing signals. Dogs proved to be very skilful in the case of the momentary pointing gestures as well as in the case of the dynamic and static ones [10, 11]. It appears to make little difference whether pointing is combined with looking at the dog or at the container [6, 9, 12].

Soproni *et al.* [11] investigated the dogs' visual communicational abilities in a series of experiments, in which dogs were presented with variations of the human pointing gesture: gestures with reversed direction of movement, cross-pointing, and different arm extensions. The use of such relatively unfamiliar variations of the pointing gesture offered the possibility also to test the animal's plasticity and capacity for generalization in understanding this visual signal. The result of this test series suggested that dogs are able to rely also on relatively novel gestural forms of the human communicative pointing gesture. Results of a more recent comparative study strengthened these findings showing that dogs are able to utilize also pointing signals by leg [13].

In addition, Szetei *et al.* [14] have found support to the hypothesis that dogs regard the pointing gesture as being a communicative act about the placing of the food, as in their experiments dogs were tended to choose the bowl pointed at by the human even when it was contradicted by direct olfactory or visual information (however they do not rely on this gesture blindly).

Besides, Miklósi *et al.* [8] has demonstrated that dogs are able to use also nodding and head turning as a cue although they are not as proficient users of these signals as they are with pointing. In the case of gazing cues dogs' performance is much lower [5, 7, 15, 16], although Miklósi *et al.* [8] showed also that some individuals can learn to use the gaze cue just like head turning.

POSSIBLE EXPLANATIONS FOR THE COMPREHENSION OF HUMAN GESTURAL CUES IN DOGS

Effect of domestication

According to Kretchmer and Fox [17] domestication is an evolutionary process, in which one popu-

lation of a species is reproductively isolated from another intentionally by humans. This reproductive isolation leads to a divergent adaptation and results in a specialization process. As a result of the changes in the selection pressures on the given species, the process of domestication produces evolutionary changes in certain aspects of the characteristic behaviour of the domesticated species just as it affects the anatomy and the morphology of the certain species as well. Such behavioural change in dogs is the decreased level of aggression for example, which is manifested also in morphological changes (*e.g.* see the morphology of the teeth).

Presumably only those species are suitable for domestication, which have a communicational system understandable for the humans. The domesticated animals had to leave their natural environment and move to a new ("domestic") environment. The most important factor of this new environment is the presence of the humans. For the domesticated animals it was advantageous in the human environment if they have proved to be controllable and have lost their fear of humans. In the case of companion animals living close relationship with the humans like dogs and cats it could have great importance to be able to live together without problems. In the course of the domestication the behaviour of dogs and cats living close to humans has been adapted to the human social environment as it is likely that humans always selected the most adaptable and tamest individuals for further breeding. The human social environment became to the natural environment of these species, in which there are complex communicational interactions with the humans.

According to the domestication hypothesis dogs (and perhaps other domesticated species) are at advantage in comprehending human communicative signals (including pointing) because the process of domestication might have selected for such skills [8, 12, 18]. To test this hypothesis Miklósi et al. [10] compared the communicative abilities of dogs with that of another domesticated species living in a qualitatively similar, close relationship with humans as companion animals, the domestic cat (Felis silvestris). Results of this direct comparison between the two species showed that both dogs and cats were able to choose on the basis of the human gesturing in a twoway object choice task, independently of the staticness and the distance of the pointing signal and there was no significant difference between their performance. In contrast, investigating the dog-human and cat-human communication from the other direction we have found that there were differences in dogs' and cats' behaviour when the subject can freely display behaviour patterns in an unsolvable situation. While dogs tended to use gaze-alternations (to look at the human and back to the hidden food) when they were unable to get the reward themselves, the cats were trying to get the food themselves and looked very rarely at the owner or at the experimenter. Putting these results together, the study of Miklósi et al. [10] found

both similarities and differences in interspecific communication in dogs and cats. However we have to note that members of various species have been reported to be able to rely on human cueing in directing their behaviour in a choice situation. Seals [19, 20] and dolphins [21] can also rely on this cue in a two way object choice test, so the high performance of cats in this study presented no surprise. But on the other hand, recent finding that domesticated goats with relatively little human contact are also able to comprehend human pointing gestures [18] also supports the domestication hypothesis. Regarding the differences in eye gazing pattern between dogs and cats, Miklósi et al. [10] suggested that the differences could be explained by a different history of domestication. One could assume that cats have not been selected for preferring eye contact with humans as exploiting this form of social interaction as a potential source of information, and they rather avoid gazing into the eyes of the humans [10].

Other comparative studies compared the communicational abilities of dogs and intensively socialized wolves. It has been shown that intensively socialized adult wolves can be trained to comprehend human pointing gestures [22], and according to the more recent findings of Gácsi et al. [23] are able to rely on such gestures also without specific experience. Findings of Gácsi et al. [23] suggested that the development of this skill provides the key difference between dogs and wolves. While 4-month-old wolf cubs do not follow the human pointing gesture, dog puppies of the same age show a rather stable performance [24]. This suggests that wolves react to a lesser degree to intensive socialisation in contrast to dogs. One can assume that genetic changes in the course of domestication allow this skill to emerge earlier in development in dogs [23].

Another way to investigate the effect of domestication is to examine systematically the role of ontogeny in the development of dogs' abilities of comprehending human social cues. In a recent study Riedel et al. [25] found that in 8-, 16- and 24-week-old dog the puppies rely on different communicative signals to find the hidden food independently of their age. These findings supported the hypothesis that domestication played a critical role in shaping the ability of dogs to follow human-given gestural cues. Wynne et al. [26] however reanalyzed the data of Riedel et al. [25] and concluded that the performance of the puppies improved with age from 6 to 24 weeks. On this basis they emphasized the role of learning during every day interactions with humans and possibly also during the experimental sessions. Wynne et al. [26] contended that the comprehension of a visual signal of an individual of a different species cannot develop independently of experiences in ontogeny.

Regarding the development of dogs' ability to use human pointing signals in a more recent study Gácsi *et al.* [23] tested 180 dogs of different ages (from 2 months to adults) in order to investigate their performance with the human distal momentary point-

ing gesture. The results, analyzed at both the group and the individual levels, showed no difference in the performance according to age, indicating that in dogs the comprehension of the human momentary distal pointing may require only very limited and rapid early learning for the full development. Interestingly, neither the keeping conditions nor the time spent in active interaction with the owner, and not even some special (agility) training for using human visual cues, had significant effect on the success and explained individual differences. The performance of the dogs was rather stable over time: also during the 20 trials within a session and even when subsamples of different ages were repeatedly tested.

Further comparative studies investigated the effects of selection for cooperation in dogs and found as well that these communicative abilities in dogs have been shaped by specific selection. Dogs of cooperative working breeds, which are involved in tasks that are based on visual communication with humans show higher performance in pointing comprehension than dogs of non-cooperative working breeds [27]. These findings on differences between certain dog breeds however also draw the attention to the fact that one cannot make simple generalizations about the effects of domestication [27].

A different line of argument: a by-product of domestication

Hare et al. [28] suggested another theory as an explanation for dogs' unusual ability for reading human communicative signals. Hare et al. [28] agreed that dogs' ability to comprehend human pointing gestures presumably have evolved during the domestication however according to them this evolution did not occur as a result of direct selection for inter-specific communicational abilities but as a correlated by-product of selection against fear and aggression toward humans (similarly as it is the case with numerous morphological and physiological features associated with the domestication process). Hare et al. [28] tested a unique experimental population of fox kits, which were selected over 45 years for approaching humans fearlessly and non-aggressively, and found that these foxes were just as skilful as dog puppies in using human proximal static pointing gestures. On the basis of these results Hare et al. [28] concluded that socio-cognitive evolution has occurred in the experimental foxes, and possibly also in domestic dogs as a correlated by-product of selection on systems mediating fear and aggression, and it is likely the observed social cognitive evolution did not require direct selection for improved social cognitive ability [28].

Effect of enculturation and socialization

Recent comparative studies have shown that living in human social environment has a strong effect on communicational abilities of different animal species considering the comprehension of human visual signals [29]. This explains the controversial results with chimpanzees in experiments examining the comprehension of the human pointing gesture. Povinelli *et al.* [30] found that chimpanzees (*Pan troglodytes*) are not able to comprehend the pointing gesture without previous training, while Itakura and Tanaka [31] found that enculturated chimpanzees and an enculturated orangutan (*Pongo pygmeus*) showed high performance in similar tasks even without previous training. Similarly controversial results were found considering the comprehension of gazing. While according to Povinelli *et al.* [30] chimpanzees are not able to comprehend the direction of human gazing as a communicative cue Itakura and Tanaka [31] found that enculturated chimpanzees performed above 90% in similar experiments.

These controversial results emphasize that besides the genetic differences, the socialization of the animals also has a great effect on the communicational abilities of the different species. Dogs' natural environment nowadays is the human family. It has been argued that dogs' unique communicational abilities toward humans can be explained by their close social relationship with the humans in the family, that is they learn to respond the human social signals in the course of their everyday life.

In the human family dogs share the social environment with human infants and so they have the chance to experience similar communicational events during their early socialization. Dogs are often described as important family members [32-34], moreover some studies on dog-human interaction describe dog-human relationship as an interspecific parental contact [35-37]. Pet-directed speech also shares similarities with 'motherese" used to talk to infants ("doggerel" see [35]).

In a series of experiments we compared the communicative skills of dogs and human infants of different ages [13]. Varying different types of pointing gesture, the first goal of this study was to find a period of human development in which children and dogs display similar levels of performance, while the second aim was to gather comparative evidence on the ability to generalize to unfamiliar gestures in both species. Our results showed little difference in the performance of 2-year-old children and dogs, while 3-year-old children's performance was high in all cases. The results also showed that to some extent all subjects were able to generalize from their previous experience to relatively novel directional gestures. These findings suggested that at least at the functional level dogs show a similar performance as 2 year-olds that can be explained as a joint outcome of their evolutionary history and their socialization in a human environment [13].

Learning through associative processes

As a possible hypothesis it has also been argued that all experimental evidence collected so far on pointing comprehension in dogs (and in other species as well) can be explained by "simple conditioning processes" [20]. It is widely accepted that dogs can learn about the significance of numerous different visual and acoustic stimuli [38]. However in the case of pointing comprehension it seems unlikely that dogs' exceptional ability to understand human visual cues would be the result only of associative learning as they can use various forms of the pointing gesture as directional cues also from a greater distance and when the cue can be seen only for a second.

Still, it has been repeatedly claimed that the successful performance is the result of rapid learning and nowadays there is a heating debate regarding the role of learning in the comprehension of human communicative cues also during the experimental sessions [25, 26]. Although the role of learning cannot be excluded in the development of dogs' communicational skills, results of numerous studies contradict this hypothesis. It was shown that in the case of socialized young wolves the extensive human contact in itself was insufficient for a good performance [24]. In addition, no evidence was found for learning over the trials and tests in independent studies with different species (goats: [18], chimpanzees: [39], seals: [19]). Besides, there is experimental evidence that if non-social cues are used for discrimination in similar settings, neither dogs [15] nor chimpanzees [40] were able to learn the discrimination task, what also provides support against the hypothesis that dogs' pointing comprehension would be a result only of associative learning.

CONCLUSION

In conclusion, at present it seems unlikely that pointing comprehension can be explained by a simple one factorial theory. The hypotheses listed above are not exclusive and might have a synergic effect. Gácsi *et al.* [27] also claimed that evolutionary and epigenetic positive feedback processes have both increased the readiness of dogs to attend to humans, providing the basis for dog-human communication.

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Conflict of interest statement

There are no potential conflicts of interest or any financial or personal relationships with other people or organizations that could inappropriately bias conduct and findings of this study.

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