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Current Trends in Canine Problem-Solving and Cognition

Ádám Miklósi[1,2] and **Enikő Kubinyi**[1,2]

[1]Department of Ethology, Eötvös Loránd University, Budapest

[2]MTA-ELTE Comparative Ethology Research Group, Hungarian Academy of Sciences, Budapest

Abstract

Dogs have occupied a central place in modern comparative cognition, partly because of their specific past and present relationship with humans. Over the years, we have gained insights about the functioning of the dog's mind, which has helped us to understand how dogs' problem-solving abilities differ from those present in related species such as the wolf. Novel methodologies are also emerging that allow for the study of neural and genetic mechanisms that control mental functions. By providing an overview from an ethological perspective, we call for greater integration of the field and a better understanding of natural dog behavior as a way to generate scientific hypotheses.

Keywords

canines; problem-solving; personality; heterochrony

The New Momentum of Dogs in Comparative Cognition

During the hundred years that followed groundbreaking research initiated by Pavlov, Thorndike, and many others, comparative cognition had not reached its full potential. In the mid-1990s, research focused mostly on humans (infants) and apes, with some attention to a few mammalian and bird species (for review, see Shettleworth, 2010). Research on dogs including observational work by ethologists (Fox, 1971) and experimental studies exploring their problem-solving abilities (Frank, 1980) helped to stimulate renewed comparative interest in the study of canines. The (re)discovery of dogs as a subject of interest was a true revolution for the field of comparative cognition, which is only now beginning to fulfil its early promise. Interestingly, this process began only recently (Hare, Call, & Tomasello, 1998; Miklósi, Polgárdi, Topál, & Csányi, 1998; Topál, Miklósi, & Csányi, 1997), without

Corresponding Author: Ádám Miklósi, Department of Ethology, Eötvös Loránd University, Budapest, Pázmány Peter, sétány 1/c, 1117 Hungary, amiklosi62@gmail.com.

Recommended Reading

Bensky, M. K., Gosling, S. D., & Sinn, D. L. (2013). The world from a dog's point of view: A review and synthesis of dog cognition research. *Advances in the Study of Behavior, 45,* 209–406. An important review on experiments aiming to reveal cognitive abilities in dogs.

Feuerbacher, E., & Wynne, C. (2011). (See References). An interesting overview of how dog research emerged in North America.

Miklósi, Á. (2014). (See References). An updated reference book on all research areas that contribute to better understanding dogs as a particular species.

Declaration of Conflicting Interests

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any particular precedents (Feuerbacher & Wynne, 2011). The development of rigorous experimental procedures and high research standards has allowed us to use methodologies that were not available before to ask important scientific questions in the study of dogs. For example:

1. The specific domestication history of dogs enables researchers to investigate how microevolution affects social cognition. Although dogs have been selected to live in an anthropogenic environment, representative populations of similar species (wolves, dingoes, feral dogs, etc.) are still available for comparative research to understand this process (Miklósi, 2014).
2. Dogs have gained the potential to share a variety of relationships with humans. Thus, the social developmental environment of dogs has been quite varied. Some dogs have a very intimate bond with their owners and are regarded as members of the family; others, such as feral dogs, keep their distance from people even if they depend on humans for their food (Miklósi, 2014).
3. Being perhaps one of the most common large-bodied mammals, dogs are available for research almost everywhere at very little cost. Thus, unlike apes for example, dogs can be widely studied by many research groups. This offers the possibility to replicate experimental results, increase reliability, and collect large data sets using various research methods (Hecht & Cooper, 2014; Stewart et al., 2015).
4. Carnivores had not been represented in comparative cognition research before the late 1990s. Although domestication affected some brain and mental functions, the dog's convoluted brain is a good model for one variant of a 100-million-year-old mammal (Andics, Gácsi, Faragó, Kis, & Miklósi, 2014).
5. The sequencing of the dog genome has offered specific tools for understanding the functioning of neural and mental mechanisms that are not possible to use with most species studied in comparative cognition (Wayne & Ostrander, 2007).
6. Being easily trainable and sociable, dogs can serve as subjects in various experimental procedures that would not be possible to use with other species. In addition, these non-invasive methods do not compromise dogs' welfare as they might that of other species.
7. Given the number and role of dogs in human societies, knowledge gained in the study of problem-solving abilities and cognition can have practical significance in applied and welfare research.

In this review, we use the framework of Nikolaas Tinbergen's four questions (Tinbergen, 1963) to understand what the function of canine cognition is, how it evolved, how it works, and how it develops.

How to Survive in an Anthropogenic Environment?

Cognitive studies focus on how perception, learning, memory, and decision-making support problem-solving behavior (Miklósi & Szabó, 2012). Although it is difficult to account for

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dogs' cognitive traits in terms of fitness as estimated by modern behavior ecology, there is a general consensus that social-cognitive skills in particular clearly contribute to dogs' survival in an anthropogenic environment.

Topál et al. (2009) proposed that the functional similarity between some human and dog behavior traits could have been selected for during convergent evolution, which happened a few million years ago in humans and tens of thousands of years ago in dogs (to some extent, in the latter case, through active selection by humans). Importantly, despite this functional similarity, "coevolution" is not assumed, partly because of the major differences in the time scale, but also because there is no evidence that dogs had any direct (selective) influence on human evolution (Miklósi & Szabó, 2012).

More recently, Miklósi and Topál (2013) introduced the concept of *social competence*, which refers to an individual's ability to display social skills that conform to the expectations of others and the social rules of the group. Rather than providing a list of functional similarities between humans and dogs, they argued that such a general perspective on social abilities provides a useful tool for conceptualizing sociocognitive functioning, as well as for considering specific social skills not in isolation but as a part of a larger system.

However, dogs' specific relationship with humans varies broadly. That is, dogs have had to have a very plastic developmental social competence (Miklósi & Topál, 2013) to maximize their fitness in different anthropomorphic environments. Fitting into a family and working as a herding sheepdog may favor different sets of social skills. The existence of a variety of human social environments probably also selected for different genotypes in dogs that are now represented partly by the existence of more than 400 dog breeds. To what extent such genetic radiation affected their sociocognitive skills remains unknown.

The Evolution of Problem-Solving Ability and Cognition in Dogs

It is very likely that the relatively short duration of domestication did not lead to specific, novel adaptations in dogs but that, rather, during their evolution some preexisting ancestral behavioral features were modified and/or changed their function. The current and original function of a characteristic can differ, as characteristics may change function over time through the co-option of existing characteristics (Bateson & Laland, 2013). For example, cooperative tendencies in wolves may have been extended to interspecific relationships (Range & Virányi, 2015) and, together with the modulation of inhibitory bias (Gácsi et al., 2005), led to the emergence of complementary cooperation in dog-human dyads (Gácsi, Szakadát, & Miklósi, 2013; Naderi, Miklósi, Dóka, & Csányi, 2001).

After many years of disagreement, most researchers now share the opinion that both evolutionary (selective) changes and developmental experience (learning) contributed to dogs' behavioral phenotype, including the ability to solve social problems in the anthropogenic environment (Hare & Tomasello, 2005; Miklósi & Topál, 2013; Udell, Dorey, & Wynne, 2010). This means that rather than referring to "dogs' evolved abilities" to adapt to the human environment, one should allude to "dogs' evolved potential" to fit into human

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social groups. This latter phrasing allows for the modifying effect of development to share in the final realization of social competence.

A further evolutionary mechanism, *heterochrony* (changes in developmental trajectories between ancestor and descendant species), also may have played an important role (Miklósi, 2014; Udell, Lord, Feuerbacher, & Wynne, 2014). Overall, socialized dogs show more pronounced interest in humans and develop human-compatible social competence earlier than wolves reared similarly. The longer and less specific sensitive period in dogs may have allowed them to learn about humans at a very plastic stage of development, which in turn may have had a long-lasting effect on their social competence. This view also has been expressed in the synergistic model of the expression of dogs' sociocognitive abilities (Gácsi, Győri, et al., 2009). Interestingly, socialized dogs may retain some flexibility in social competence later in life, and for this they need much less reinforcement from the anthropogenic environment in comparison to socialized wolves. Abandoned shelter dogs' re-socialization and ability to form new attachment relationships may constitute an example of such flexibility (Gácsi, Topál, Miklósi, Dóka, & Csányi, 2001).

Wilkins, Wrangham, and Fitch (2014) proposed that depigmentation, floppy/reduced ears, shorter muzzles, smaller teeth, a smaller brain, more frequent estrous cycles, curly tails, and, importantly, delayed adrenal-gland maturation and heterochronic delay in sympathetic reactivity might be explained by a mild neural-crest-cell deficit during embryonic development. This could prolong the sensitive period for positive contact with humans (Belyaev, Plyusnina, & Trut, 1985), which has lifelong effects on docility and cognition.

Although comparative studies are valuable in testing hypotheses, they have their limits. Perfect similarity between the groups is difficult to achieve, and extra-genetic inheritance processes (e.g., epigenetic impacts on gene expression) may also play a role. Therefore, despite similar socialization, not only genetic differences but the history of previous generations affects research findings.

How Does It Work? Methods in Studying Behavioral Mechanisms

We have come a long way from the traditions of anecdotes, but some research in comparative cognition still relies on vague concepts and ambiguous terms (e.g., "theory of mind") rather than on a scientifically based and ethologically sound experimental approach and method.

Recently, several researchers have proposed that the study of sociocognitive traits in dogs can provide a new animal model for certain human clinical conditions. For example, Overall (2000) pointed out parallels between human psychiatric states and problem behavior in dogs (e.g., compulsive behavior and separation anxiety). There has been an increased interest in utilizing dogs as an animal model of cognitive aging (Gilmore & Greer, 2015; Szabó, Gee, & Miklósi, 2015). These models rely heavily on the assumption that dogs' mental functioning can be investigated at different levels of causality, including cognition, neurobiology, and genetics.

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Cognition

Our understanding of mental representation in dogs has been greatly enhanced by the ability to follow the eye movements of dogs. Eye tracking allows for the monitoring of attention, including interest, preference, and also some aspects of planning. Dogs' eye movements follow the gaze of their human partner if he or she displays communicative intent (Téglás, Gergely, Kupán, Miklósi, & Topál, 2012), and dogs scan the human face differently depending on the emotion displayed (Somppi, Törnqvist, Hänninen, Krause, & Vainio, 2014).

Perceptual processes such as recognition, matching, and categorization are important features of cognitive functioning. The application of touch-screen devices may lead to deeper insight into how dogs deal with social and communicative stimuli. The screen serves as a medium for presenting different kinds of stimuli for the dogs to choose from. As a first step, dogs are trained to associate correct responses with a food reward. After particular training experience, dogs are presented with a new choice for the first time, which reveals the underlying reasoning process. For example, Müller, Schmitt, Barber, and Huber (2015) showed that dogs can match upper and lower parts of a novel face if both are displaying the same emotional expression.

A novel method allows for the exploration of how dogs represent novel agents (unidentified moving objects [UMOs]) if these agents show a simple behavior pattern and have a tendency to engage socially. In these experiments, dogs are exposed to a UMO (a remote-controlled car), which moves autonomously and helps the dog get food that is beyond its reach. After a few such experiences, the dogs start to treat the UMO as a social partner (Gergely et al., 2015), and they extend this experience to other contexts (i.e., they tend to copy the UMO's choice of food even if this choice is suboptimal; Abdai, Gergely, Petró, Topál, & Miklósi, 2015).

Neurobiology

The application of non-invasive methods to study neural functioning in dogs could revolutionize the field of comparative neurobiology. For example, an overall pattern of brain activity can be obtained by placing electrodes on specific locations of the skull; non-invasive polysomnography used to measure dog sleep physiology can provide electroencephalogram (EEG) data that are directly comparable to those of humans (Kis, Szakadát, et al., 2014); and the local activation pattern of the brain in response to stimulation can be revealed by fMRI. In this way, unrestrained, awake dogs can be used to map the response to auditory stimuli in a comparative setting (Andics et al., 2014; Andics et al., 2016), to reward signals (Berns, Brooks, & Spivak, 2013) and the signal source (Cook, Spivak, & Berns, 2014), and to scents (Berns, Brooks, & Spivak, 2015).

Domestication may have affected the pattern and activity of dogs' neurotransmitters (Arons & Shoemaker, 1992; Saetre et al., 2004). Most recent investigations have focused on the role of oxytocin in dog-human interactions because this neuropeptide has been believed to promote affective tendencies. Social interaction, like gazing and/or petting, seem to release oxytocin in both species (Nagasawa et al., 2015), but this phenomenon is a consequence of a

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mammalian homology supported by developmental plasticity and not the result of coevolution (Kekecs et al., 2016). Intranasally administered exogenous oxytocin has increased looking back at the human standing behind the dog during the threatening approach test (Hernádi et al., 2015). This observation was interpreted as a specific effect of the neuropeptide whereby it increases affiliative tendencies toward familiar social partners. After learning that food can be found at one location ("positive" location) but not at another location ("negative" location) on the opposite side of the room, dogs approached a new location faster after exogenous oxytocin administration if it was placed halfway between the positive and negative locations (Kis, Hernádi, Kanizsár, Gácsi, & Topál, 2015). The performance of the dogs in this so-called cognitive-bias test suggested an increased positive expectation in ambiguous locations.

Local changes in body temperature (caused by inflammation or stress) can be detected by infrared thermography (IRT). This non-invasive method, which involves using a special video camera, is based on measuring minute differences in the infrared light spectrum emitted by the body of the dog. Some results have suggested that IRT may be a useful tool for investigating emotional psychogenic stress in dogs (Travain et al., 2016).

Genetics

In humans, the major cognitive domains, memory in particular, show relatively high heritability (Harris & Deary, 2011). Several candidate genes have been tested for association with behavior traits in dogs (Hall & Wynne, 2012), but research has not tested for such associations in the cognitive domain, with the exception of a study by Hori, Kishi, Inoue-Murayama, and Fujita (2013), who found that the dopamine receptor D4 gene (*DRD4*) is associated with gazing toward humans in an unsolvable-problem task. However, the small sample size and the varied genetic background of the dogs limit the reliability of this result. The oxytocin receptor gene (*OXTR*) polymorphism was also found to be associated with gazing toward humans in an unsolvable-problem task (Kis, Bence, et al., 2014).

Metabolite profiling could also help in identifying genes and molecular pathways involved in canine behavior and performance (Puurunen, Tiira, Lehtonen, Hanhineva, & Lohi, 2016). Epigenetics (alterations in DNA without sequence changes; Jensen, 2015) and transcriptomics (analysis of the set of all RNA molecules; Nätt et al., 2012) would also be of interest.

How Does It Develop? Missing Links to Behavioral Development

One cannot get a full understanding of cognitive abilities without studying the effects of development. However, development is difficult to study for methodological and practical reasons. For example, performance on problem-solving tests depends not only on actual mental skills but also on collateral factors like perceptual abilities, temperament, and motivation, which also change in parallel during development. Thus, it is not surprising that the best source of information on behavioral development to date is a book by Scott and Fuller (1965) published more than 50 years ago. Not only do we lack information about how learning abilities and memory develop in young dogs, but there is also little knowledge about the development of social and communicative behaviors, including the emergence of attachment between dogs and their owners (but see Gácsi et al., 2001; Topál et al., 2005).

The response of dogs to human pointing gestures provides an exception. However, even in this case, methodological variations and differences in the social exposure of the dogs have led to disagreements among researchers (Hare et al., 2010; Udell, Dorey, & Wynne, 2008; Wynne, Udell, & Lord, 2008). Dog puppies seem to be able to perform a two-alternative choice based on variations in human hand gestures from around 2 to 4 months of age (Gácsi, Kara, Belényi, Topál, & Miklósi, 2009; Riedel, Schumann, Kaminski, Call, & Tomasello, 2008). Interestingly, wolf pups do not show comparable performance at the same age but are successful at about 1 year of age (Gácsi, Győri, et al., 2009). Detailed behavioral observation reveals that young wolves do not tolerate being held by an experimenter and look less often and only for a short time at the experimenter. Thus, the difference between the two species may not be in mental ability but rather in temperament.

Studying the effect of development on puppies is also difficult because there is often great variability in the rearing environments of dogs. Some of them may have restricted contact with humans, others are overindulged, and many participate in various training activities. At the moment, we do not know how such experience influences problem-solving abilities. Many social ecological factors influence the individual development of dogs, and these factors have been influenced by both conspecific and heterospecific social partners over multiple generations (Bateson & Laland, 2013). In the case of dogs, humans play a specific role in constructing their developmental environment.

The Fifth Question: Do dogs have a personality?

The interest in dogs has also increased attention to individual differences, an area that has been rather neglected (and typically viewed as “noise”) in the study of laboratory animal populations. However, individual behavioral differences, which are relatively stable in time and across contexts (cf. personality), have gained significance because from a functional point of view they can be regarded as behavioral strategies (personality traits; Gosling, 2001). In particular circumstances, individuals with different behavioral strategies may coexist in the same population or specific environments may favor individuals showing particular strategies. Many recent experimental studies and reviews have been directed at determining the primary personality traits of dogs (Fratkin, Sinn, Patall, & Gosling, 2013), but little attention has been paid to whether and how personality traits affect problem-solving performance.

Individual variation in problem-solving behavior and cognition (intelligence) also has not been studied in dogs in any detail. This is quite unfortunate, because dogs could provide a good animal model for separating genetic and environmental effects on many mental abilities. Arden and Adams (2016) attempted to measure components of dog intelligence by subjecting 68 Border Collies to a series of problem-solving tasks. Although this study found some evidence for a human-analog “*g* factor,” as the authors suggested, there are still many unanswered questions concerning the methodology, the population tested, and the test battery used, just as has been the case with humans.

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Conclusions

Intensive research with dogs has brought them to the forefront of comparative cognition research. However, this brief summary of research has also shown that there is a need for more integration. In addition, there are many areas in which research is still lacking and improved methodologies are needed. Dogs offer an unprecedented case for combining ultimate and proximate approaches, but it is important that dogs not be regarded as laboratory animals. Researchers who study dogs should acquire a background of ethological knowledge about dog behavior when they propose to study dogs and other canines.

The new and rapidly developing non-invasive technologies developed for humans are now being used to measure similar traits in dogs. This gives researchers who study cognitive mechanisms in dogs a great advantage over colleagues investigating other species.

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