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Is cognition the secret to working dog success?

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Dogs and humans have long cooperated in remarkable ways. For thousands of years, dogs have improved the outcome of human hunting, helped guard people and livestock and detected and warned of danger humans cannot perceive (Hare & Woods, 2013). Through careful breeding, rearing and training, this cooperative relationship has been further enhanced in today's working dogs that help solve a host of societal problems. Guide dogs help lead people without sight or hearing. Detector dogs use olfactory cues to find bombs, contraband, diseases and even endangered animals. Assistance and therapy dogs aid children and adults with physical disabilities or need of emotional support (Rodriguez et al, 2020). All of these jobs are evidence that dogs' relationship with humans remains essential in today's society.

Because of working dogs' success, there is a growing demand for a larger supply of dogs for all these different job types (Otto, Cobb, & Wilsson, 2019). To match the growing need, scientists are investigating how enhanced breeding, selection, and training of working dogs can improve their supply and success. Since working dogs rely heavily on their cognitive skills, meeting this challenge is one of the most exciting questions in animal cognition. If we can identify cognitive traits that make success possible and then reliably measure individual variability in these traits, we will not only unlock secrets of the canine mind, but also develop tools designed to get more highly qualified dogs working to help those in need (MacLean & Hare, 2018; Lazarowski et al., 2018).

Here we review work that launched a new era of research focused on dog cognition. We start with the identification of dogs' unusual social skills and explain how this basic research led to the latest approaches for applying cognitive theories and methods to the challenge of enhancing working dog programs. Both the basic and applied work suggest this is a particularly exciting moment for researchers and students studying dog cognition.

Unusual Minds

Before 1998, understanding cooperative communicative intentions appeared to be a *unique* maturational accomplishment of human infants. Between 9–12 months of age, infants begin to understand that the perceptions and intentions of others can differ from their own (Carpenter, Nagell, & Tomasello, 1998). Critical evidence for this transition is the comprehension and production of pointing gestures. Infants not only follow the pointing gestures of adults, but they understand the cooperative-communicative intentions behind them (Tomasello & Farrar, 1986; Tomasello et al., 2007). This way, as infants, we already can rapidly learn from others and acquire cultural knowledge - including language.

On the contrary, nonhuman primates in their natural interactions and in captive experiments do not readily comprehend helpful human gestures – unless they have been raised with intense exposure to humans (Wobber et al, 2014). Understanding cooperative communicative intentions appeared to be a *unique* maturational accomplishment of human infants. This led to the prediction that no other nonhuman animal would show infant-like understanding of human gestures. It was a surprise to psychologists when domestic dogs use human gestures skillfully in experiments. In 1998, two papers were published demonstrating that dogs use these gestures to find hidden food and objects (Miklosi et al, 1998; Hare et al, 1998). Follow up studies demonstrated how similar dogs' ability to use gestures is to that of humans.

All of this work was heavily influenced by theories and methods used by developmental psychologists studying human infants. A simple search game used with infants became a standard method: food or a toy is hidden in one of two hiding locations. The experimenter shows the dog they are hiding a reward but does not allow the dog to see in which location (e.g. the empty hiding spot is sham baited). This game is repeated such that a dog's ability to locate the reward reliably across repeated trials can be compared to chance levels (i.e. 50% correct across trials if two hiding spots are used; Miklösi et al., 1998).

In playing this search game with a range of pet dogs, a number of low-level explanations were immediately ruled out. Without a visual gesture from the experimenter, dogs were unable to find food or toys, and their chance performance ruled out the use of olfactory cues (Agnetta et al., 2000; Bhattacharjee et al., 2020; Hare et al., 1998; Riedel et al., 2008; Rossano, Nitzschner, & Tomasello, 2014; Soproni, Miklósi, Topál, & Csányi, 2001; Stewart et al., 2015). Dogs were able to use a variety of gestures – including novel ones (Agnetta et al 2000; Reidel et al, 2008; Rossano et al, 2014), and their responses also did not rely solely on orienting to the motion of the arm being extended. Dogs can use the gestures of strange humans and even the body posture of another dog "pointing" toward the correct hiding locations (Hare & Tomasello, 1999). This level of flexibility is far more similar to that displayed in human infants than nonhuman primates – including mother reared great apes. It led our team and others to conclude that the comprehension of gestures by our dogs is unusual and human-like (Hare & Tomasello, 2005).

Cognitive Origins

The unusual nature of dog's understanding of our gestures created interest in understanding the origins of these abilities both from an ontogenetic and phylogenetic perspective.

Dog puppies' ability to read human gestures emerges early in development, regardless of their rearing history (Hare et al, 2002; Reidel et al, 2008). They seem prepared to comprehend humans, even with varying levels of human contact. Both feral village and assistance dog puppies use pointing and novel gestures on their first trial around the age of weaning (Bhattacharjee et al., 2020; Bray et al, 2020).

Phylogenetically, all dog breeds and populations that have been studied perform above chance levels in human gesture tasks (Horschler et al 2019). However, within the species, there is variability in adult dogs' success in following human social cues. For example, even New Guinea singing dogs and dingoes, who have not been under intense artificial selection, are skilled at understanding human gestures when searching (Wobber et al, 2009; Smith & Litchfield, 2010). Like, chimpanzees, some adult wolves can learn to comprehend human gestures through practice and intense exposure to humans, but they do not show the early emerging skills observed in dog puppies (Udell et al 2012; Lampe et al, 2017; Viranyi et al 2008; Gasci et al, 2009). In a recent comparison, dozens of wolf puppies were hand reared from ten days after birth and exposed to humans 24 hours a day (i.e. they slept together with their caregivers). Even with intense exposure to humans, they were less likely to approach a human, use human gestures, and make eye contact than dog puppies with far less human exposure (Solomans et al, 2021).

The early emerging understanding of human gestures in dogs, but not wolves, is likely a result of domestication. Fox kits experimentally selected for friendly behavior toward humans (i.e. approaching, wagging tail, initiating physical contact, etc.) are also as skilled at using human gestures as dog puppies. Fox kits from the control line perform similarly to wolf pups (Hare et al, 2005). The fox work suggests that as the domestication process was initiated and wolves were selected to interact with humans, this same selection led to enhanced abilities to cooperatively communicate with humans (Hare & Tomasello, 2005; see also Hernádi et al 2012). Later artificial selection on dogs likely enhanced these cooperative communicative abilities as a result of direct selection on social skills (Wobber et al 2009).

Social Genius

With the initial discovery of unusual cooperative communicative understanding in dogs, researchers began examining other forms of cognition. This work has revealed both cognitive flexibility and constraints. Dogs do not just comprehend but also produce signals. For example, in some contexts, dogs intentionally communicate when they need help. When dogs were shown a locked box they had previously opened to obtain food, they quickly made eye contact with a nearby human. When the human did not help them, some dogs pawed at the human or alternated gaze between the person and box while barking (Miklosi et al, 2003; MacLean & Hare, 2018). On the other hand, when a human is not present, dogs do not use communicative behaviors, emphasizing dogs' sensitivity to human attentional states (Hare et al, 1998; Kaminski et al., 2017).

Some dogs (or breeds) may be particularly gifted at learning object labels. When playing fetch, several border collies have demonstrated the ability to learn the names of new objects using the principle of exclusion. After the dog learned the label for a familiar object, a human introduced a novel object and asked the dog to retrieve it. When this novel label was used, dogs made an inference and retrieved the unfamiliar object instead of the familiar one. After only a few repetitions, they continue to bring back this same object in response to the same label. Other than humans, no other species has demonstrated the ability to rapidly match and learn object labels in this way (Kaminski et al, 2004; Pilley & Reid, 2011). Dogs can also learn to spontaneously imitate some novel actions demonstrated by humans. Using the “do as I do” training method, dogs learn to approximate the actions they see a human demonstrate with their own bodies. For example, without any shaping of behavior, after hearing the command “do as I do”, dogs will spin in a circle or place a ball in a basket after their first observation of a human doing these simple actions (Topál et al., 2006). They also can reproduce actions they have seen demonstrated after significant delays – suggesting they may recall past actions episodically (Fugazza, Pogány, & Miklósi, 2020).

Dogs also use their eyes and bodies to strengthen their bond with us. Experimental evidence suggests that dogs and humans that make the most eye contact have the strongest bonds. This has been linked to the release of oxytocin – both humans and dogs show increases in levels of circulating oxytocin when making eye contact or after positive physical interactions (i.e. petting; Romero et al 2014). The use of eye contact is likely aided by the evolved eye morphology of dogs. Morphological study revealed that dogs, but not wolves, have enhanced eye muscles (AU101 muscle) that function to reveal more white sclera tissue. These muscles are thought to have evolved during domestication to facilitate the interspecific oxytocin loop and bonding between human and dog (Waller et al., 2013). Support comes from the higher rate of adoption for shelter dogs that show a higher baseline rate of flexing the AU101 muscle in the presence of strange humans (Kaminski et al., 2019). In addition, a study of dog facial expressions showed that dogs produce more facial movements when a human is attending to them versus not (Kaminski et al., 2017). Thus, it appears dogs evolved to understand and communicate with humans.

In addition to communicating using their own faces, dogs also pay close attention to human facial expressions. They are able to discriminate between happy, angry, and neutral expressions (Nagasawa et al. 2011; Albuquerque et al. 2016; Morisaki et al. 2009), and they exhibit behavioral reactions to different human emotions. For example, one study showed that dogs avoided looking at angry human faces and paid closer attention to faces showing fear (Deputte & Doll, 2011). Dogs also provided empathic-like “comforting behaviors” such as sniffing, nudging, licking to strangers who were pretending to cry instead of approaching their owners (Custance & Mayer 2012). These social skills make dogs especially suited to live as close human companions, as well as therapy animals and in other service capacities.

However, dogs do not always use their understanding of humans to our benefit. Dogs are also sensitive to when a human is watching them. They are more likely to disobey a command when a human has their back turned or eyes closed than when they are being watched (Brauer et al, 2003). For instance, smaller dogs, in particular, are more likely to take forbidden food when a human has their eyes closed or face covered (Horschler et al 2019). The dependency of dogs on human social information is also so strong that it can mislead them; dogs will follow a human gesture pointed toward an incorrect hiding spot instead of searching for food where they recently saw it hidden (Stewart et al, 2015). Dogs will even search a hiding location a human touched last over one they saw repeatedly baited (Topal et al 2009; Kupan et al, 2011; Kis et al, 2012). This tendency to prioritize human information or instructions can badly interfere with some types of work (i.e. detector dogs; Lit, Schweitzer, & Oberbauer, 2011). Moreover, the unusual social skills of dogs seem limited to cooperative-communicative context. When compared to chimpanzees in a social reversal learning paradigm (i.e. two humans acted as the hiding locations with one or the other holding food in their hand), dogs were utterly unremarkable. In the first trial of the social task, chimpanzees were able to inhibit what they had previously learned, while dogs were no faster in the social than nonsocial tests (Wobber & Hare, 2009). Moreover, dogs may be limited in their ability to assess what a human can or cannot see when following their gestures (MacLean et al, 2014).

Finally, a number of nonsocial skills have been investigated in dogs. Dogs can solve an array of problems using their memory or self-control (Bray et al, 2014; 2015). They do have some basic understanding of causality as well. At least in some situations, dogs appreciate that solid objects cannot pass through each other, but their appreciation of connectivity and gravity are more limited. For example, dogs do not seem to understand that when two objects are connected (i.e. by a leash), they act together. While a dog can learn this relationship through shaping and practice, they show little ability to generalize what they learn in one context to another novel situation (Hare & Woods, 2013). These findings have implications for the limits of flexible problem solving to expect in these context when training working dogs.

Cognitive Profiles

Studies with dogs are not constrained by sample size like those with primates and other large animals (Hare et al, 2001; MacLean et al, 2014). This means techniques initially developed to study individual differences in human infant cognition can be used to examine dogs (Herrman et al, 2007; 2010). Test batteries that include a dozen or more cognitive measures have been used in conventional laboratory settings and by citizen scientists. Our research group designed the Dog Cognitive Test Battery or DCTB (see Fig 1) that includes as many as two dozen social, non-social and general cognitive measures. We tested hundreds of dogs with the DTCB and used a factor analysis to discover that individual differences in performance across the tests could not be explained by a single general factor. Variability in performance was best explained by up to six different factors corresponding to domains of intelligence including: social referencing, inhibition, cooperative-communication, working memory, perceptual bias, and discriminatory ability (MacLean et el 2017). A similar pattern is found when thousands of dogs were tested using dognition.com by citizen scientists. This citizen science project allows people to test their dogs at home on a related set of tasks to the DCTB. Analyzing this large data set we again find a strong signal for domains of cooperative-communication, inhibition and working memory (Stewart et al, 2015; Horschler et al, 2019; Gnanadesikan et al, 2020).

Test batteries have also begun to be developed for use with dog puppies (Lazarowski et al., 2019; 2020). Our own team modified the DCTB for use with puppies. We then used this developmental battery of cognitive tasks with puppies as young as two months of age – or shortly after weaning (Bray et al, 2020). Longitudinal analysis of over one hundred and fifty dogs revealed that individual variation in cognition was trait-like. Furthermore, individual variation observed in almost two-hundred puppies was correlated with cognitive variation observed in the same dogs as adults. This means that, to a certain degree, cognitive differences between individuals are stable across the lifetime – although this stability is stronger in some measures than others (Bray et al, 2020b). This work promises to point to cognitive profiles in puppies that might predict training outcomes as adults. These profiles could be used as a powerful tool to select the most promising puppies for working jobs, potentially increasing the graduation rate in training programs.

Further analysis suggests that the individual variability observed in test batteries is highly heritable. As much as 40–50% of individual variability in skills using gestures, memory and inhibition are explained by genetic factors in both the citizen science and university lab tested dogs (Gnanadesikan et al, 2020 a, b, c). Using a genome wide association, it was further demonstrated this same individual variability was associated with genes implicated in brain development and function (Gananadesikan et al, 2020 b). Together with work demonstrating the heritability of individual differences in emotional reactivity (MacLean et al, 2019), these findings point to new approaches to breeding dogs with enhanced emotions and cognition related to their success working with humans.

Results from cognitive batteries have also allowed for the first large-scale breed comparisons of cognition. Over seventy dog breeds tested on ten cognitive measures by citizen scientist were examined. On most measures there was little difference explained by breed. However, larger dogs performed better with human gestures and tasks requiring inhibition and memory. Smaller dogs were more skillful at stealing food based on whether a human was watching them after forbidding them to take it (Horschler et al 2019). Interestingly, though, recent neuroscientific evidence suggests that strong neuroanatomical differences between breeds is best explained by breed and not by body, skull, or brain size. In addition, these anatomical differences correlate with behavioral specializations such as hunting, guarding, and companionship. Phylogenetic analysis of these results suggests that these specializations are the result of recent selection pressure on dogs by humans (Hecht, et al., 2019). These findings highlight the success of selection for working performance as well as a need for further exploration into cognitive variations between breeds.

A factor analysis was also conducted to revisit the idea that dogs’ cognitive abilities are human-like. Large samples of dogs, human infants and chimpanzees were all tested on the same eight cognitive tasks – with half being social and half being nonsocial measures. For both dogs and human infants, performance on one social task predicted performance on another, but did not associated with skill on nonsocial tasks. Chimpanzees, on the other hand, showed no association between the social and nonsocial tasks. This means dogs have a more human-like organization of their cognitive abilities than chimpanzees, with clear differentiation between social and nonsocial abilities (MacLean et al, 2017). Even the individual level dogs appear more human-like on measures of cooperative-communication than our closest primate relatives.

Finally, test batteries have also begun to be used to enhance the selection and training of working dogs. In a large set of assistance and detector dogs that were tested with the DCTB before training, performance was associated with a number of the cognitive measures. These initial associations were used to develop predictive models for a separate set of dogs tested before training. These models were able to predict, with up to 95% accuracy, which dogs were most likely to succeed in training before training began (MacLean & Hare, 2018; see also Bray et al., 2020). Cognition tests batteries, once further refined, may provide a powerful tool in the future for increasing success rates for working dog training programs, especially if they can predict the success early on in young working dog puppies (Lazarowski et al., 2018; MacLean & Hare, 2018; Bray et al, 2020a,b).

Working Future

This is an exciting moment in the field of animal cognition. Dogs offer a powerful way to answer new and old questions while providing a sustainable research model (i.e. allowing for replication, large scale studies, application to the real world and a range of funding opportunities). Dogs' unique relationship with humans and the evolution of social skills that rival even our closest relatives make them ideal candidates for the jobs that are crucial to human society, as well as fascinating subjects for studying behavior. The future is bright for both the study of dog cognition and the prospect for enhancing breeding, selection, and training of working dogs due to the discoveries we make about the minds of our best friends. In particular, future research on training dogs using social learning models instead of simple individual instrumental learning techniques could be particularly promising (i.e. Slabbart & Rasa, 1997; Pongrácz et al, 2001; Topál et al., 2006). Integrating any advances with an understanding of development will also allow for the largest impact on working dog programs; the earlier in a dog's life we can predict their future abilities, the more likely we can provide them the support they need to be successful (Bray et al, 2020b). The exciting challenge remains how we can use all we learn to improve the ability of dogs to do all the important jobs they continue to help us with while protecting their welfare while they do it. That way we can be their best friends too.

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