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Individual differences in cooperative communicative skills are more similar between dogs and humans than chimpanzees



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Keywords: chimpanzee cognition communication convergence domestic dog human individual differences test battery By 2.5 years of age humans are more skilful than other apes on a set of social, but not nonsocial, cognitive tasks. Individual differences in human infants, but not chimpanzees, $Pan\ troglodytes$, are also explained by correlated variance in these cooperative communicative skills. Relative to nonhuman apes, domestic dogs, $Canis\ familiaris$, perform more like human infants in cooperative communicative tasks, but it is unknown whether dog and human cognition share a similar underlying structure. We tested 552 dogs in a large-scale test battery modelled after similar work with humans and nonhuman apes. Unlike chimpanzees, but similarly to humans, individual differences in dogs were explained by correlated variance in skills for solving cooperative communicative problems. Direct comparisons of data from all three species revealed similar patterns of individual differences in cooperative communication between human infants (N=105) and domestic dogs (N=430), which were not observed in chimpanzees (N=106). Future research will be needed to examine whether the observed similarities are a result of similar psychological mechanisms and evolutionary processes in the dog and human lineages.

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The cultural intelligence hypothesis proposes that human cognition is unlike that of other species primarily as a result of humans' early emerging skills for reasoning about the social world (Herrmann, Call, Hernandez-Lloreda, Hare, & Tomasello, 2007). Beginning around 9 months of age, human infants exhibit a suite of social cognitive skills including gaze following and the production and comprehension of cooperative communicative gestures (Carpenter, Nagell, & Tomasello, 1998, Tomasello, 1999). These nascent abilities subsequently scaffold processes such as language acquisition, symbolic reasoning and social learning during the first years of life (Tomasello, 1999). The cultural intelligence hypothesis predicts that while adult human minds may differ from those of other animals in many respects, these differences arise largely because of early emerging social cognitive skills for sharing, and following and directing the attention of others, which support the cultural acquisition of knowledge across cognitive domains.

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The phylogenetic predictions of the cultural intelligence hypothesis were tested in a large-scale comparison of human infants and nonhuman apes tested with a comprehensive battery of cognitive tasks (Herrmann et al., 2007). Whereas nonhuman apes and 2.5-year-old infants performed similarly on tests of physical cognition (e.g. object permanence, spatial reasoning, number discrimination), already by 2 years of age, humans outpaced other apes with regard to social cognition (e.g. communication, theory of mind, social learning). These findings were recently corroborated in a 3-year longitudinal study of human infants and age-matched bonobos, *Pan paniscus*, and chimpanzees, *Pan troglodytes*. Specifically, the earliest differences in cognition between human children and nonhuman apes related to measures of social cognition, with differences in physical cognition unfolding later in development (Wobber, Herrmann, Hare, Wrangham, & Tomasello, 2014).

Building on these findings, psychometric analyses revealed surprisingly divergent patterns underlying individual differences in human infants and chimpanzees (Herrmann, Hernandez-Lloreda, Call, Hare, & Tomasello, 2010). Specifically, individual differences in human infants were best described by a three-factor model

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including clusters of skills for (1) solving physical problems, (2) spatial reasoning and (3) social cognition. In contrast, although chimpanzees shared a (presumably homologous) factor for spatial reasoning with humans, only human infants had a unique factor corresponding to social cognition (Herrmann, Hernandez-Lloreda et al., 2010). Therefore, although chimpanzees are remarkably socially sophisticated (Goodall, Lonsdorf, Ross, & Matsuzawa, 2010; de Waal & Tyack, 2003), the organizational properties of their cognition may be markedly different than those of humans.

Research with domestic dogs, Canis familiaris, has challenged the notion that humans' early emerging social skills are completely unique to our species (Hare & Tomasello, 2005). For example, dogs exploit a wide range of cooperative communicative signals more similarly to humans than nonhuman apes (Brauer, Kaminski, Riedel, Call, & Tomasello, 2006; Hare & Tomasello, 2005; Hare, Brown, Williamson, & Tomasello, 2002; Kaminski & Nitzschner, 2013; Téglás, Gergely, Kupán, Miklósi, & Topál, 2012), use fast mapping to learn object labels (Kaminski, Call, & Fischer, 2004; Pilley & Reid, 2011) and commit the same socially mediated perseverative error as human infants in the Piagetian A not B task (Topál, Gergely, Erdöhegyi, Csibra, & Miklósi, 2009). Importantly, these similarities between dog and human cognition appear to be restricted to the social domain. Whereas dogs outperform nonhuman apes in cooperative communicative social tasks, they are far less skilled than apes when solving physical problems (Brauer et al., 2006). To explain these findings, the domesticated cognition hypothesis (Hare, Wobber, & Wrangham, 2012; Hare et al., 2002, 2005) proposes that humans and dogs underwent similar selective pressures for 'survival of the friendliest', leading to convergent skills for cooperative communication in both species (Hare, 2017).

A central prediction of this hypothesis is that the underlying structure of dog social skills for cooperative communication should resemble that of humans. That is, individual differences in dog cooperative communication should exhibit similar patterns of covariance to human infants, and this pattern should be more similar between dogs and humans than between either of these species and nonhuman apes. Therefore, the critical test of this hypothesis requires a comprehensive dog cognition test battery, similar to that used with human infants and nonhuman apes, and a heterogeneous sample of hundreds of dogs to identify the correlational structure underlying individual differences. To test this prediction we examined a sample of 552 dogs tested in the dog cognition test battery and compared the correlational structure of individual differences in dogs to similar data from human infants and chimpanzees (Herrmann, Hernandez-Lloreda et al., 2010).

METHODS

The dog cognition test battery (DCTB) was developed based on the tasks in the primate cognition test battery (PCTB; Herrmann et al., 2007; Herrmann, Hernandez-Lloreda et al., 2010; Wobber et al., 2014) as well as other previously published studies of dog cognition (Supplementary Material). In total, the DCTB included 25 different problem-solving tasks designed to assess skills for reasoning about the social and physical world, as well as domaingeneral cognitive processes. The battery was administered in four ~1 h test sessions per subject.

Subjects

We conducted the DCTB with three different populations of dogs including two working dog populations (assistance dogs, N = 215; explosive detection dogs, N = 222) as well as a relatively heterogeneous sample of pet dogs (N = 115) (Supplementary

Material). Working dogs (Labrador retrievers, golden retrievers, and Labrador × golden crosses) were tested in indoor rooms at their training facilities and pet dogs were tested in a similar indoor environment at the Duke Canine Cognition Center. Pet dogs were recruited through a database of local dog owners in the Raleigh-Durham region of North Carolina, U.S.A., and owners received free parking and a dog 'diploma' for their participation. The three populations of dogs varied with respect to their training and housing conditions. Specifically, both working dog populations lived in a kennel environment and participated in daily training as assistance dogs (i.e. working with people with disabilities) or explosive detection work. In contrast, the pet dogs lived in human households and had no formal training beyond basic obedience. All testing was strictly voluntary, and dogs were free to stop participating at any time (see Supplementary Material for participation requirements for each task). Subjects participated for food and toy rewards, and were not deprived of food or water. All dog testing procedures were approved by the Institutional Animal Care and Use Committee of Duke University (IACUC protocol numbers: A303-11-12 and A138-11-06).

We compared the patterns of individual differences in dogs to those of a population of 106 chimpanzees and 105 2-year-old human children previously tested in a similar cognitive test battery (Herrmann et al., 2007). All chimpanzee subjects were living and tested at African sanctuaries (Ngamba Island Chimpanzee Sanctuary, Lake Victoria, Uganda, and Tchimpounga Chimpanzee Sanctuary, Republic of Congo). All of the apes were born in the wild and came to the sanctuary after being confiscated at an early age (~2—3 years old) as a result of the trade in apes for pets and bushmeat. When quantitatively compared across a range of cognitive tasks, sanctuary apes performed as well as or better than conspecifics living in zoos or conspecifics that had been mother-reared (Wobber & Hare, 2011; Wobber et al., 2014). Human subjects were recruited from primarily middle-class households in a medium-sized city in Germany.

Design

Similar to previous test batteries (Herrmann, Hare, Call, & Tomasello, 2010; Herrmann et al., 2007; Wobber et al., 2014), the order of tasks was the same for all subjects. Although this design cannot eliminate the possibility of order effects (in terms of how participation on a given task affects performance on subsequent measures), it ensures consistency across subjects, permitting direct comparisons of individual differences across tasks. For all object choice tasks (i.e. which required subjects to choose between two locations when searching for objects or food), the location of the reward was counterbalanced between trials and the same location was never baited for more than two consecutive trials, unless otherwise noted.

MATERIALS

All dogs were tested in indoor rooms furnished with a rubber floor mat (306×246 cm) marked with the starting locations for the experimenters (E1, E2, E3), the subject and the locations of objects for each task (see Supplementary Fig. S1). In the majority of object choice tasks (exceptions specified below), food was hidden under cylindrical plastic containers (17×16 cm). For object choice tasks, E1 occluded the baiting/sham baiting process using a cardboard occluder (54×34 cm). For memory tasks, a large freestanding cardboard occluder (237×46 cm) was used to occlude the hiding locations during the delay. For other tasks requiring E1 to place the occluder on the ground while performing a manipulation behind it, a slightly smaller freestanding cardboard occluder (122×46 cm) was used.

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