



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



Evan L. MacLean<sup>a,\*</sup>, Esther Herrmann<sup>b</sup>, Sunil Suchindran<sup>c</sup>, Brian Hare<sup>d,e</sup>

<sup>a</sup> School of Anthropology, University of Arizona, Tucson, AZ, U.S.A.

<sup>b</sup> Department of Comparative and Developmental Psychology, Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany

<sup>c</sup> Center for Applied Genomics and Precision Medicine, Duke University, Durham, NC, U.S.A.

<sup>d</sup> Evolutionary Anthropology, Duke University, Durham, NC, U.S.A.

<sup>e</sup> Center for Cognitive Neuroscience, Duke University, Durham, NC, U.S.A.

## ARTICLE INFO

### Article history:

Received 26 April 2016

Initial acceptance 13 July 2016

Final acceptance 12 December 2016

Available online 24 February 2017

MS. number: A16-00375R

### 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.

© 2017 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

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.

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

\* Correspondence: E. MacLean, School of Anthropology, University of Arizona, P.O. Box 210030, Tucson, AZ 85721, U.S.A.

E-mail address: [evanmaclean@email.arizona.edu](mailto:evanmaclean@email.arizona.edu) (E. L. MacLean).

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, Erdőhegyi, 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 domain-general 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.

## Rewards

To accommodate both food- and toy-motivated dogs, the reward consisted of a small piece of food (approximately  $1 \times 1$  cm; see below) placed next to a small toy (both items were hidden together on all trials unless otherwise noted). Food rewards were chosen based on their different properties (i.e. smell, size, etc.) as they related to each task. Rewards included Jerky Treats (for all object choice tasks), Zuke's Mini Naturals (for sensory bias, odour discrimination and causal reasoning, auditory condition), or peanut butter or Kong Stuff'n (for laterality, object manipulation). If a dog would not eat the food items specified above, alternative foods (Yummy Chummy Salmon Treats, Vienna sausage, or owner-supplied alternatives) were used as needed. The toy rewards were chosen based on the task and preference or size of the dog, with the goal of consistently maintaining motivation to search or play. For the majority of tasks and dogs the toy was a Kong® Classic, or, for certain tasks (specified below), a tennis ball. For 42 dogs, the toy was an Extra-Small Plush Kong® Duckie. For pet dogs, the toy was sometimes a small toy provided by the owner.

## Procedure

Like the primate version of this battery, the majority of our tests used an object choice paradigm. In tests of social cognition, subjects were required to infer the location of the hidden reward using cooperative communicative gestures (e.g. pointing, gazing, reaching) whereas tests of physical cognition required the subject to remember or infer the reward's location through information about the physical environment (e.g. object permanence, spatial transpositions, visual and auditory causal properties, spatial memory). In addition, we implemented a wide variety of other previously published problem-solving tasks measuring processes related to executive function, navigation, perspective-taking, communication, emotional contagion and laterality biases. The majority of tasks were scored live, and interobserver agreement (assessed by an independent scorer from video) was excellent for all measures (Supplementary Table S3). Detailed descriptions of the battery design, experimental tasks, task origins, scoring procedures, participation and abort criteria are included in the Supplementary Material. Below we briefly describe each task in its order of administration.

### Warm-ups: Hiding–finding

Each day of the battery, prior to participating in object choice tasks, dogs were required to complete a series of warm-up trials. These trials familiarized dogs with the basic hiding–finding paradigm used in the majority of our tests and ensured that subjects were motivated and capable of meeting basic task demands. Warm-ups consisted of four stages (phases 1–4) of increasing difficulty, and dogs were required to meet a criterion at all stages to advance to the main battery tests (Supplementary Material).

### Battery tasks

**Affect discrimination.** This test measured a dog's preference to approach an unfamiliar human based on positive or negative affective cues from the human's tone of voice (based on Vas, Topál, Gácsi, Miklósi, & Csányi, 2005). Two experimenters sat on the floor and alternated turns vocalizing towards the dog. The 'friendly' experimenter spoke in a high-pitched affiliative tone whereas the 'unfriendly' experimenter spoke in a sharp low-pitched tone. On each trial we measured which individual (if either) the dog approached. Approaches to the 'friendly' experimenter received a score of 1, approaches to the unfriendly experimenter received a

score of –1, and no approach received a score of 0. The dependent measure was the average score across trials. Thus, scores greater than 0 reflect a tendency to approach the 'friendly' experimenter whereas negative scores reflect a tendency to approach the 'unfriendly' experimenter.

**Arm pointing.** This task measured a dog's ability to use an arm pointing gesture to locate a hidden reward (based on Hare, Call, & Tomasello, 1998; Miklósi, Polgárdi, Topál, & Csányi, 1998). The experimenter stood equidistantly between two containers and pointed to the baited container using the arm closest to it, with index finger extended. The dependent measure was the percentage of trials that a subject's first search was to the baited container.

**Visual discrimination.** This task measured a dog's ability to learn an arbitrary visual discrimination that predicted the reward's location (based on Head, Callahan, Muggenburg, Cotman, & Milgram, 1998; Range, Aust, Steurer, & Huber, 2008). Three containers were placed in an array. Two of the containers (the distractors) were short blue cups, and the other (the target) was a tall yellow cylinder. On each trial the reward was hidden (without the subject seeing) under the target container, but the locations of the target and distractors varied between trials. The dependent measure was the percentage of trials that dogs first searched in the target container.

**Cylinder.** This task measured a dog's ability to inhibit a prepotent motor response to reach directly for a visible reward on the other side of a transparent barrier (based on Bray, MacLean, & Hare, 2014; MacLean, Hare, et al., 2014). In warm-up trials, a cylinder covered with opaque fabric was placed on the ground. Subjects saw the experimenter place the reward inside the cylinder and were required to detour to the side of the apparatus to retrieve the reward from within. On test trials, the procedure was the same, however the cylinder was transparent. Thus, dogs were required to resist a prepotent response to approach the reward directly (bumping into the cylinder) in favour of a detour response. The dependent measure was the percentage of trials that dogs correctly performed the detour response without bumping into the transparent cylinder.

**Detour navigation.** This task measured a dog's ability to take the shortest route around an obstacle (based on Pongrácz et al., 2001). A V-shaped fence was arranged such that one arm of the fence was twice the length of the other. The dog was walked around the fence to familiarize the dog with the spatial layout. The dog was then positioned outside the vertex of the V-shaped fence, and an experimenter on the other side called the dog to come to her. On each trial we scored whether the dog reached the experimenter via the shorter route (2 points), the longer route (1 point), or whether the dog failed to detour the fence entirely (0 points). The dependent measure was the average score across trials.

**Spatial perseveration.** This task measured a dog's ability to inhibit a previously successful motor pattern when the environment changed such that this response was no longer effective (based on Osthaus, Marlow, & Ducat, 2010). A fence divided the test room such that there was a gap at the left side of the fence, but not the right. In warm-up trials dogs were familiarized with detouring around the fence to their left to reach the experimenter at the other side. Before test trials and while the dog was out of the room, the fence was moved so that the gap was now on the right. In the test trials we scored whether dogs initially tried to detour around the fence to the left (location of previous gap in fence, but now visibly closed) or right (new location of gap, visible to dog). The dependent

measure was the percentage of trials that dogs first moved towards the right (open) side of the fence.

**Social referencing.** This task measured a dog's tendency to look at a human's face when a social game was interrupted (based on Merola, Prato-Previde, & Marshall-Pescini, 2012; Nagasawa, Kikusui, Onaka, & Ohta, 2009). The experimenter engaged the dog by playing with a small stuffed animal. After 10 s of play the experimenter interrupted the game and held the stuffed animal against the ground. During the interruption dogs could visually monitor the toy (on the ground) or could seek social information by looking to the experimenter's face. The dependent measure was the mean percentage of time that dogs looked at the experimenter's face during these interruptions.

**Gaze direction.** This task measured a dog's ability to use the experimenter's gaze direction to locate a hidden reward (based on Hare et al., 1998; Miklósi et al., 1998). The method was identical to the arm-pointing task with the exception that the experimenter simply turned her head to look at the baited container.

**Causal reasoning.** This task measured a dog's ability to use visual and auditory information to infer the location of a reward (based on Brauer et al., 2006). In visual trials, two circular cloths were placed on the floor equidistant from the dog. The experimenter then showed the dog a bucket containing the reward and behind an occluder placed this bucket under one of the two cloths. Dogs were required to infer where the bucket containing the reward was hidden based on which of the two cloths was visually displaced by the bucket underneath. In auditory trials, two empty paint cans were placed on the floor equidistant from the dog. The experimenter then approached and baited or sham-baited each can behind an occluder. After baiting or sham-baiting each container, the experimenter lifted the container and shook it briefly. The baited container rattled audibly when shaken, whereas the unbaited container was silent. The dependent measure was the proportion of trials that dogs chose the baited container.

**Unsolvable task.** This task measured a dog's tendency to persist at an unsolvable task, or to solicit social help in this context (based on Miklósi et al., 2003). In warm-up trials, the experimenter placed the reward inside a transparent container with the lid loosely affixed. Dogs were familiarized with dislodging the container's lid to retrieve the reward. In test trials, the experimenter latched the container's lid in place such that it could not be opened. The dependent measures were the mean duration of time that the dog spent manipulating the container or looking at the experimenter during the unsolvable trials.

**Working memory.** This task measured a dog's ability to recall the spatial location of a hidden reward after varying temporal delays (based on Dore, Fiset, Goulet, Dumas, & Gagnon, 1996; Fiset, Beaulieu, & Landry, 2003). Three containers were placed in an array in front of the dog. The experimenter visibly hid a reward in one of the containers and then occluded them using a large free-standing occluder. After a delay of 20, 40 or 60 s, the occluder was removed and the dog was allowed to search. The dependent measure was the percentage of trials that a dog chose the baited container.

**Sensory bias.** This task measured whether a dog prioritized visual or olfactory information when these senses were pitted against one another (based on Szeteci, Miklósi, Topál, & Csányi, 2003). Two plastic funnels were placed in front of the dog with their spouts

facing upwards. In test trials, the experimenter created the illusion that only a single reward was being hidden, while in reality, both funnels were baited on every trial. Dogs then received a visual cue that the reward was in one location (the experimenter briefly lifted the funnel to visually reveal the reward underneath) and an olfactory cue that the reward was in the other location (dogs were allowed to smell the reward through the top of the funnel). The dependent measure was the percentage of trials that dogs chose the visually cued container.

**Marker cue.** This task measured a dog's ability to infer the location of hidden reward when the experimenter used an arbitrary physical marker to communicatively indicate the reward's location (based on Agnetta, Hare, & Tomasello, 2000; Riedel, Buttelmann, Call, & Tomasello, 2006). This task was identical to the arm-pointing task with the exception that the experimenter showed the dog a small blue block and placed this block on top of the baited container. The dependent measure was the percentage of trials that dogs chose the baited container.

**Odour discrimination.** This task measured a dog's ability to discriminate and remember which of two containers contained food after smelling the contents of each container (based on Szeteci et al., 2003). Two funnels were positioned on the floor with their spouts facing upward. The handler then walked the dog by each funnel allowing the dog to smell through the top of the funnel for 3 s. In the first half of trials, one funnel was empty whereas the other contained the reward. The second half of trials were identical with the exception that both funnels also contained a masking odour (peach flavoured tea bag). The dependent measure was the percentage of trials that dogs chose the baited funnel.

**Perspective-taking.** This task measured a dog's tendency to obey or disobey a command depending on whether the experimenter was watching the dog (based on Call, Brauer, Kaminski, & Tomasello, 2003). In 'sit' trials, the experimenter stood 1 m from the dog and commanded the dog to sit. In one half of trials the experimenter faced the dog while giving the command whereas in the other half he had his back to the dog. We recorded the number of trials that dogs sat in each condition. In 'stay' trials, the experimenter placed a piece of food between himself and the dog and firmly told the dog to stay while gesturing prohibitively. In one half of trials, the experimenter remained watching the dog for the next 30 s, and in the other half he turned his back to the dog. We recorded the number of trials that dogs took the prohibited food in each condition. The dependent measure was a composite metric averaging the scores from the sit and stay trials. Higher scores reflect a greater tendency to disobey the experimenter more often when his back was turned.

**Spatial transpositions.** This task measured a dog's ability to track the location of a baited container over the course of a variety of spatial transpositions (based on Rooijackers, Kaminski, & Call, 2009). Two containers were placed on the ground, one of which was visibly baited in front of the dog. The containers were then moved in one of three ways: (a) no cross: both containers were moved in the same horizontal direction; (b) one cross: one container was moved to the other side of the first, while the first container remained stationary; (c) two cross: both containers switched locations, each ending up where the other began. The dependent measure was the percentage of trials that dogs chose the baited container.

**Transparent obstacle.** This task measured a dog's ability to inhibit approaching the experimenter directly when she called the dog

urgently from the opposite side of a transparent barrier (Bray, MacLean, & Hare, 2015). The dog started outside the vertex of a V-shaped transparent barrier, with the experimenter facing the dog on the other side. Before the test the handler walked the dog around the entire apparatus to familiarize the dog with the path around the obstacle. In test trials, the experimenter held the reward and called the dog to come to her in a high-pitched and urgent tone of voice. The dependent measure was the percentage of trials that a dog successfully navigated around the barrier without first bumping into its transparent exterior.

*Memory - distraction.* This task measured a dog's ability to remember the location of a hidden reward following varying temporal delays during which a human intentionally distracted the dog (based on Dore et al., 1996; Fiset et al., 2003). The task was identical to the working memory task except that we used only two delays (20 and 40 s), and during the delay a human stood between the dog and the containers, and pet the dog's head while singing to the dog to distract the dog from the task. The dependent measure was the percentage of trials that dogs chose the baited container.

*Contagious yawning.* This task measured whether a dog yawned contagiously when hearing an audio recording of an unfamiliar human yawning (based on Harr, Gilbert, & Phillips, 2009; Joly-Mascheroni, Senju, & Shepherd, 2008; O'Hara & Reeve, 2011; Silva, Bessa, & de Sousa, 2012). Auditory stimuli were obtained from Silva et al. (2012) because these stimuli were shown to induce contagious yawning in a previous study with dogs. The stimuli consisted of an audio recording of a human yawning and a control stimulus consisting of the yawning clip played backwards. The stimuli were presented in an ABBA design (A = yawning, B = control) and we recorded the number of yawns that dogs exhibited during each condition. The dependent measure was the number of yawns a dog made during the yawning condition minus the number of yawns in the control condition.

*Reaching.* This task measured a dog's ability to use a reaching gesture to infer the location of a hidden reward (based on Brauer et al., 2006). This task was identical to the arm-pointing task except that the experimenter sat in a chair and reached effortfully towards the baited container before the dog was allowed to choose.

*Inferential reasoning.* This task measured a dog's ability to infer the location of a hidden reward through the principle of exclusion (based on Erdőhegyi, Topál, Virányi, & Miklósi, 2007). Two containers were positioned in front of the dog. The experimenter approached the containers successively, briefly lifting the unbaited container to reveal that there was nothing underneath and simply grasping the baited container for the same amount of time. The dependent measure was the percentage of trials that dogs chose the baited container.

*Odour control trials.* This task served to verify that subjects could not locate the hidden reward using olfaction (based on Brauer et al., 2006; Hare et al., 1998; Miklósi et al., 1998). This task was identical to the arm-pointing task except that the experimenter provided no social cue prior to the dog's search. The dependent measure was the percentage of trials that dogs chose the baited container.

*Laterality (first step).* This task measured which forelimb (left or right) a dog preferred to use when initiating a step off of a platform, as well as the consistency of this preference across trials (based on Tomkins, Thomson, & McGreevy, 2010). A handler walked the dog onto a small platform and positioned the dog in a sitting position. The experimenter stood in front of the dog and called the dog to

her. On each trial we coded which paw the dog led with when stepping off the platform. The dependent measure for this task was an absolute laterality index, defined as  $|((R - L)/(R + L) \times 100|$  (Batt, Batt, & McGreevy, 2007).

*Laterality (object manipulation).* This task measured which forepaw (left or right) a dog preferred to use when physically manipulating an object, as well as the consistency of this preference across trials (based on Batt et al., 2007; Branson & Rogers, 2006). A small section of PVC pipe was filled with a soft food reward (e.g. peanut butter) and placed on the floor. From video we coded which paw the dog used to stabilize the tube as the dog attempted to extract the food. The dependent measure was the absolute laterality index defined above.

*Rotation.* This task measured whether a dog encoded the spatial location of a hidden reward using egocentric or allocentric spatial cues (based on Fiset, Gagnon, & Beaulieu, 2000; see Fig. S2). Two containers were placed in front of the dog. In familiarization trials, the experimenter visibly placed a reward in the container to the dog's left and the dog was allowed to search. In test trials, the dog started from the opposite side of the room. In these trials, the experimenter created the illusion that only a single reward was being hidden, while in reality, both funnels were baited on every trial. The dependent measure for this task was the percentage of trials that a dog choose the reward to the dog's left during test trials (the same location that was baited during familiarization trials, but to the opposite side of the dog in test trials). Thus, higher scores reflect an allocentric search bias whereas lower scores reflect an egocentric search bias.

*Retrieval.* This task measured a dog's tendency to retrieve an object and return it to the front of the experimenter (based on Gácsi, Miklósi, Varga, Topál, & Csányi, 2004; Hare et al., 1998; Horn, Virányi, Miklósi, Huber, & Range, 2012). The task began by the experimenter engaging the dog in a game of fetch. After this warm-up the experimenter stood at a central location and threw the ball in front of her. On half of trials she remained facing the dog, whereas on the other half of trials she turned her back to the dog. On each trial, we coded the dog's behaviour according to the following scoring system: 0 = the dog did not retrieve the object; 1 = the dog retrieved the object but did not bring it back to within arm's reach of the experimenter; 2 = the dog retrieved the object but brought it to the experimenter's back (i.e. where the experimenter could not see the dog); 3 = the dog retrieved the object and brought it in front of the experimenter (i.e. where the experimenter could see the dog). Scores of two or three required that the dog returned to within arm's reach of the experimenter, standing either behind or in front of the experimenter, respectively. The dependent measure for this task was the average score across trials.

## RESULTS

Overall performance on each task is shown in Table 1. To explore patterns of individual differences, we first conducted an exploratory factor analysis using the 'psych' package (Revelle, 2014) in the R environment (v.3.1.0; R Core Team, 2015). To limit the number of missing values requiring imputation, we first restricted data to subjects missing data for no more than one task in the battery, resulting in a data set of 433 dogs that were used for this analysis. The remaining missing values for these subjects (0.16%) were imputed using a nearest-neighbour approach. Prior to factor analysis, we first assessed sampling adequacy using the Kaiser–Meyer–Olkin measure of sampling adequacy (KMO). Five variables had KMOs below the recommended minimum (0.5) for

**Table 1**  
Mean performance and standard deviation for each task in the battery

	Mean	SD
Affect discrimination	0.12	0.37
Arm pointing	70.15	22.45
Causal reasoning	54.91	17.39
Contagious yawning	0.10	0.56
Cylinder	60.61	33.69
Detour navigation	1.46	0.38
Gaze direction	64.97	21.51
Hiding-finding	3.9	0.94
Inferential reasoning	46.87	19.02
Laterality: First step	50.95	29.08
Laterality: Object manipulation	35.00	27.37
Marker cue	85.87	17.16
Memory – distraction	55.76	22.35
Odour control trials	45.07	20.53
Odour discrimination	54.22	12.13
Perspective-taking	4.19	17.33
Reaching	68.45	22.67
Retrieval	2.15	1.02
Rotation	45.67	35.23
Sensory bias	72.07	20.02
Social referencing	29.00	25.14
Spatial perseveration	59.44	24.33
Spatial transpositions	41.15	10.49
Transparent obstacle	80.31	26.60
Unsolvable task (look at experimenter)	9.29	8.98
Visual discrimination	42.78	19.75
Working memory	62.52	21.21

See Methods and Supplementary Material for the dependent measure for each task.

exploratory factor analysis (laterality (first step), laterality (object manipulation), detour navigation, yawn contagion, perspective-taking) and were thus removed before further analysis (Budaev, 1998; Kaiser, 1970; Kaiser & Rice, 1974). We then conducted parallel analysis to determine the number of factors to extract (Horn, 1965). Comparison of the eigenvalues from actual data to randomly resampled and simulated data suggested a six-factor solution, which was implemented with a varimax factor rotation. The KMO measure supported sampling adequacy for this model (overall KMO = 0.64), and Bartlett's test for sphericity was significant ( $\chi^2_{210} = 745.06$ ,  $P < 0.001$ ), indicating that the correlations between measures were sufficient for factor analysis. In this initial model, several variables did not load on any specific factor (loadings  $< |0.30|$ ; Hair, Anderson, Tatham, & Black, 1998; Stevens, 2012), so following the recommendations of Osborne and Costello (2009), we refitted the model excluding these variables.

Factor loadings and the complete linkage dendrogram for tasks in the final model are shown in Fig. 1. The first factor (6% common variance) was loaded positively by two tasks measuring the duration of dogs' gaze to a human's face either when confronted with an unsolvable task or following the disruption of a dyadic social game (social referencing). These tasks were similar in that dogs could attend to either an object or a human face, but they differed in terms of the context for these responses. Specifically, in the unsolvable task, dogs faced an instrumental problem that they had previously solved individually and they could persist at the task themselves or seek human help. In contrast, the social referencing task established a dyadic social activity at the outset, and when the activity was disrupted, the dogs could monitor the object or seek social information by looking at the human's face. The second factor (8% common variance) was loaded positively by three tasks designed to assess spatial memory (hiding–finding, working memory, memory (distraction)). In all three tasks subjects witnessed the experimenter hide food in one of multiple locations before they were allowed to search, but the delays during which subjects were required to store this information in memory, the number of possible hiding locations and whether subjects were

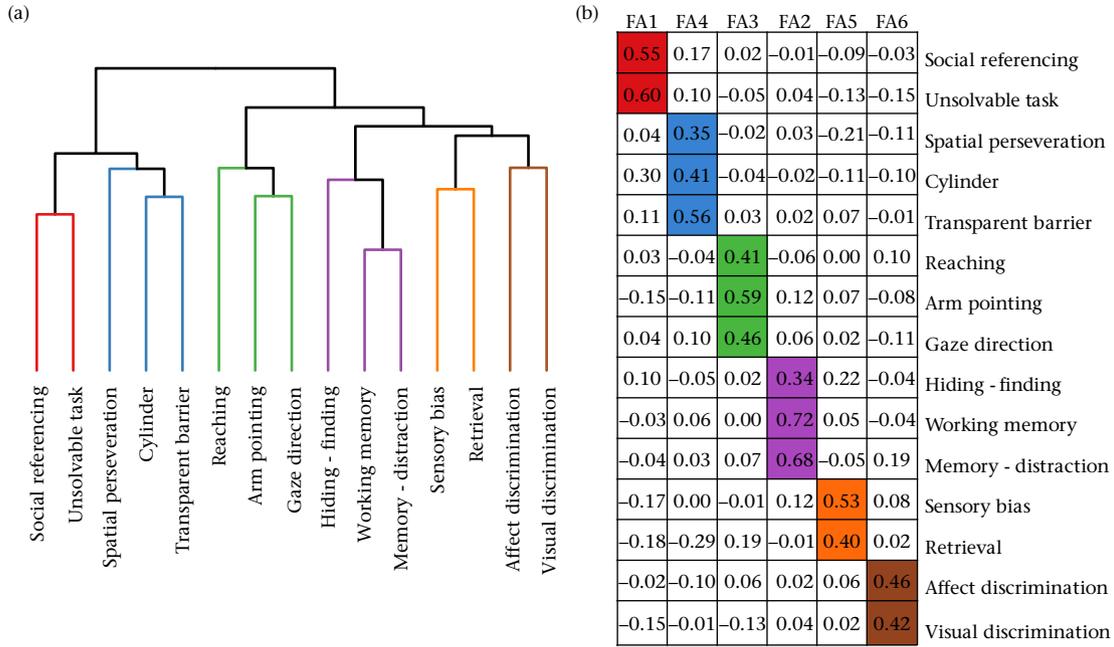
exposed to a distracting stimulus during the delay varied between tasks (see [Supplementary Material](#)). The third factor (5% common variance) was loaded by three tasks designed to assess sensitivity to cooperative communicative social gestures (pointing, gaze direction, reaching). Critically, this correlated cluster of sociocognitive abilities has been implicated as a key organizational property of human cognition that distinguishes our species from our other ape relatives.

Factor 4 (5% common variance) was loaded by three tasks designed to measure inhibitory control (spatial perseveration, cylinder, transparent barrier). These tasks required subjects either to resist a prepotent response to move directly towards a visible reward by detouring around an obstacle, or to inhibit a previously successful motor pattern when the environment changed such that this response was no longer effective. The fifth factor (4% common variance) was loaded by two tasks measuring visual/olfactory bias and object retrieval skills, and captures differences between the detector dogs and other dog populations in the sample. Finally, the sixth factor (3% common variance) was loaded by two discrimination tasks, one requiring dogs to use information about the physical properties of an object regardless of its spatial location in an array of objects (visual discrimination) and the second requiring dogs to use information about tone of voice, regardless of the speaker's identity (affect discrimination).

Collectively, individual differences in dog cognition were best explained by multiple independent factors and are unlikely to be attributable to individual differences in 'general intelligence' (Stewart et al., 2015). A central finding from this analysis is that unlike previous studies with nonhuman apes, but similarly to human infants, individual differences in dogs were characterized by correlated variance in skills for cooperative communication. Therefore, not only do dogs outperform nonhuman apes in these cooperative communicative contexts (Brauer et al., 2006), but these abilities covary across individual dogs similarly to human infants.

Despite this similarity between humans and domestic dogs, the test batteries for these species included different tasks, precluding quantitative species comparisons across the full range of tests in either battery. Therefore, we identified a subset of eight object choice tests (four social and four nonsocial) that were implemented similarly with human infants, chimpanzees and domestic dogs (see [Supplementary Table S5](#)). The four social tasks required subjects to use (1) pointing gestures, (2) gaze direction, (3) an arbitrary communicative marker and (4) a reaching gesture to locate a hidden reward. The four physical cognition tasks required subjects to (1) recall the spatial location of a hidden reward, (2) follow the spatial transpositions of a baited container in an array of distractors and infer the location of the reward using (3) visual and (4) auditory causal properties.

To test whether individual differences on these tasks could be explained by two factors related to social and nonsocial cognition, we initially used confirmatory factor analysis (CFA) within each species. Subjects missing data for any of the eight cognitive variables were excluded from analysis, yielding final sample sizes of 430, 105 and 106 for domestic dogs, human children and chimpanzees, respectively. All confirmatory factor analyses (CFAs) were fitted with 'Mplus' (v.7.2) using weighted least squares. These models revealed similar patterns in human infants and domestic dogs ([Supplementary Table S6](#)), but the statistical model did not converge for chimpanzees (data not shown), precluding comparison with the other two species. Therefore, to compare the correlational structure underlying individual differences across species, we (1) examined the complete linkage dendrograms for the eight cognitive tasks across species and (2) used hierarchical clustering and a bootstrapping procedure to assess the stability of variable clustering within species (Andreeff et al., 2008; Kerr & Churchill,



**Figure 1.** (a) Complete linkage dendrogram for cognitive tasks with significant loadings in the exploratory factor analysis with domestic dogs ( $N = 433$ ). Variables with significant positive loadings on each of the six factors have colour-coded branches indicating which factor they correspond to. (b) Factor loadings for each variable that loaded significantly on at least one factor. Variables loading  $\geq 0.30$  are colour-coded to indicate the factor (FA) they correspond to.

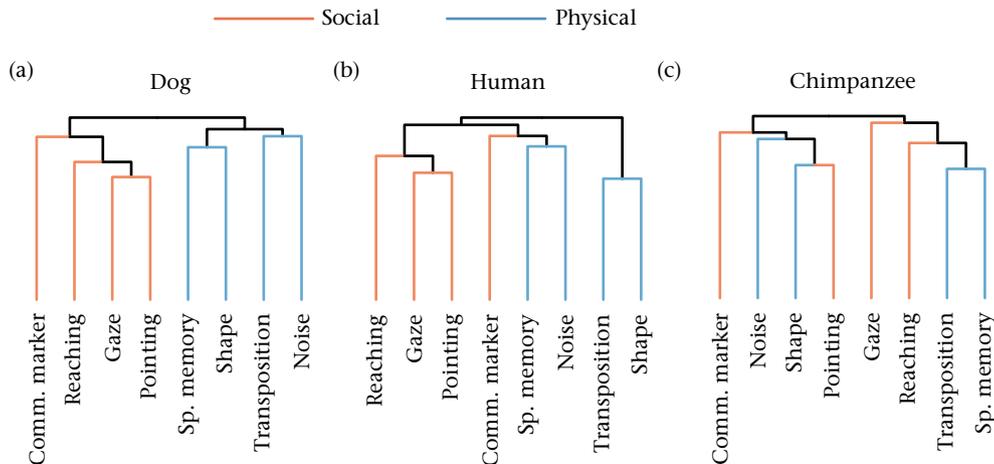
2001; see [Supplementary Material](#)). Complete-linkage analyses revealed a cluster consisting strictly of social cognitive tasks in both dogs and humans but not in chimpanzees ([Fig. 2, Supplementary Fig. S4](#)). While this cluster contained all four social measures for dogs, it contained only three of the social measures (pointing, gaze and reaching measures, but not the arbitrary communicative marker) for humans.

In the bootstrapping procedure (10 000 iterations), variables were divided into two clusters using a distance metric based on the Pearson correlation, and we calculated the proportion of iterations that pairs of variables clustered together. In contrast to pairwise correlation values, this approach reveals the robustness with which pairs of variables cluster together when a two-cluster model is imposed on the data. Methods were implemented in the R environment ([R Core Team, 2015](#)) using modified code from the Object-Oriented Microarray and Proteomic Analysis (OOMPA) library (MD Anderson Cancer Center, Houston, TX, U.S.A.). These analyses

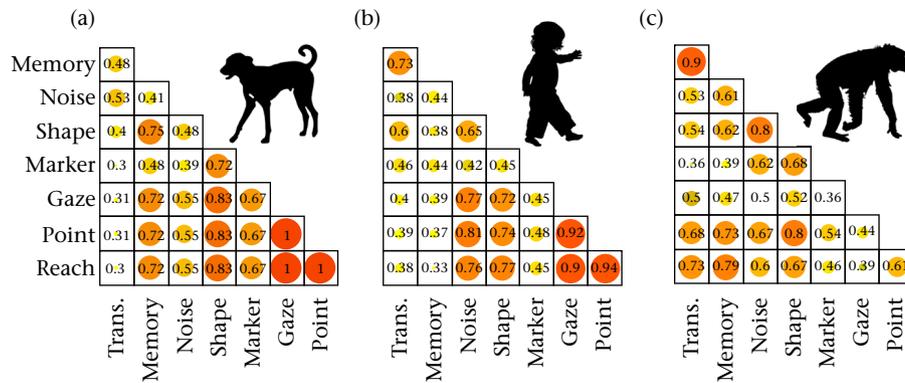
revealed robust similarities between human infants and domestic dogs that were not observed in chimpanzees ([Fig. 3](#)). Specifically, in both dogs and human infants, three sociocognitive measures (responses to gazing, pointing and reaching) clustered together  $\geq 90\%$  of the time (range 90–100%), whereas these variables clustered together much less frequently in chimpanzees (mean = 48%, range 39–61%). As an additional measure of sensitivity within dogs, we also conducted these analyses separately for each of the three dog populations and found similar results. Within each population these measures clustered together  $>80\%$  of the time ([Supplementary Material, Fig. S3](#)).

**DISCUSSION**

Our comparative analysis of individual differences in domestic dogs, human infants and chimpanzees reveals striking socio-cognitive similarities between dogs and humans. Specifically,



**Figure 2.** Complete linkage dendrograms for eight cognitive measures implemented similarly with (a) dogs, (b) human infants and (c) chimpanzees. Red branches correspond to measures of social cognition (e.g. gaze, point following) and blue branches correspond to measures of physical cognition (e.g. spatial memory, causal reasoning).



**Figure 3.** Results from a bootstrapped hierarchical clustering analysis in which eight variables were divided into two clusters. Panel values show the proportion of iterations that pairs of variables clustered together in (a) dogs, (b) human children and (c) chimpanzees. Trans. = spatial transposition.

individual differences in both domestic dogs and human infants are characterized by correlated variance in skills for cooperative communication that are independent from skills for reasoning about the physical world. Thus, dog cooperative communicative comprehension resembles that of human infants not only at the species level (Hare & Tomasello, 2005), but also at the level of individual differences. Because these skills do not covary similarly in chimpanzees, it is unlikely that the observed dog–human similarities represent a cognitive homology, jointly inherited from a common mammalian ancestor (for additional preliminary comparisons with bonobos and orang-utans see [Supplementary Material](#)). Furthermore, although developmental experience can influence an individual's cognitive phenotype, and likely played a role for all our subjects, there are several reasons why it is unlikely that rearing history is the primary explanation for the species differences we observed. First, the social cognitive skills shared by dogs and humans begin to emerge early in dog ontogeny (Riedel, Schumann, Kaminski, Call, & Tomasello, 2008), and their expression does not require intensive exposure to humans (Hare et al., 2002). Second, the chimpanzees in our sample have regular contact with human caregivers, and many of these individuals had intensive experience with human surrogate mothers beginning in infancy. Although this type of rearing is atypical for chimpanzees, these subjects had lifelong experience interacting with humans, and by some definitions could be considered 'enculturated' (Russell, Lyn, Schaeffer, & Hopkins, 2011; for additional analyses including rearing history see [Supplementary Material](#)). Third, the patterns we observed in dogs were present across three dog populations with different rearing and training histories, inclusive of dogs living in human homes and kennels. Lastly, although the use of human experimenters in comparative tests of social cognition has previously been critiqued (Herrmann, Call, Hernandez-Lloreda, Hare, & Tomasello, 2008; de Waal, Boesch, Horner, & Whiten, 2008), several studies reveal no difference in apes' use of social cues depending on whether subjects interacted with a human or conspecific (Brauer, Call, & Tomasello, 2005; Hare & Tomasello, 2004; Itakura, Agnetta, Hare, & Tomasello, 1999). Therefore, one plausible explanation for the similarities between human infants and domestic dogs is that of convergent evolution, in which similar cognitive systems for navigating cooperative social environments evolved independently in both lineages.

An ultimate explanation for these findings is that similar selective pressures on temperament, specifically selection for high social tolerance and reduced aggression, occurred both during human evolution (Cieri, Churchill, Francisus, Tan, & Hare, 2014; Herrmann et al., 2007) and dog domestication (Gácsi et al., 2009; Hare & Tomasello, 2005; Hare et al., 2002; MacLean & Hare,

2015; Topál et al., 2009). Selection for these traits has been linked to sociocognitive evolution in experimentally domesticated populations (Hare et al., 2005) and was likely an important precursor for the evolution of more complex forms of cooperative communication in both humans and dogs. Following shifts in temperament, 'revealed variance' (West-Eberhard, 2003) in cognitive skills for cooperative communication may have come under direct selection in both lineages, ultimately leading to convergent cooperative communicative social skills that are used both within and between these species. Importantly, this hypothesis predicts that cooperative communicative abilities do not arise primarily in response to the informational demands of social complexity (which are likely most similar between humans and panins), but rather as a result of selection on emotional systems permitting highly cooperative forms of social interaction.

The domesticated cognition hypothesis proposes that human-like aspects of dog social cognition arose during dog domestication and postdate the dog–wolf divergence. This possibility is suggested by data revealing species-level differences between dogs and wolves on cooperative communicative tasks (Gácsi et al., 2009; Hare et al., 2002; Miklósi et al., 2003; Virányi et al., 2008; but see ; Udell, Dorey, & Wynne, 2010). However, it is also possible that these aspects of dog cognition were inherited from the grey wolf, *Canis lupus*, a species characterized by cooperative breeding and hunting. Therefore, a more accurate dating of the hypothesized convergence will require similar research with hundreds of wolves to probe the structure of individual differences in this species. Similarly, if indeed unique to dogs, it remains unknown whether these characteristics evolved early in dog domestication, prior to active artificial selection by humans, or whether these traits are the product of more recent selection associated with the origins of modern breeds. Notably, although our pet dog population contained a wide variety of purebred and mixed-breed dogs, both of our working dog samples consisted exclusively of retriever breeds. Given that, in a previous eye-contact task, retrievers differed from other breeds (Jakovcevic, Elgier, Mustaca, & Bentosela, 2010), it will be important to extend the study of individual differences to other breed groups in future research.

One could also hypothesize that similarities in the socialization processes for humans and domestic dogs are the driving force for the observed species similarities in individual differences. Specifically, both dogs and children who develop in a human environment may have similar learning opportunities that result in common patterns of individual differences across species. Of course, if developmental exposure were all that was required, we should expect similar patterns in other species raised with close human contact. Our findings with human-socialized chimpanzees and bonobos do not support this hypothesis, and raising apes in a

human family as if they were dogs or children is as dangerous as it is unethical. It is unlikely that enough individuals of these different species could ever be raised with similar enough experiences to completely refute such an extreme environmental stance. However, comparable data sets from other species that can safely and ethically be raised in human environments will provide important future data relevant to the role of socialization with humans in explaining these findings.

Importantly, we do not discount the possible effects of development in human environments, and instead see this as an integral part of how complex communicative skills emerge. As a result of domestication, dogs are prepared to live alongside and engage with humans in ways that are not common for nondomesticated species. Indeed, the domesticated cognition hypothesis specifically proposes that evolutionary changes to the socioemotional systems that allow dogs to integrate naturally with human populations are part and parcel to why dogs exhibit such communicative flexibility. In this sense, even when nonhuman apes and dogs are similarly socialized by humans, dogs may be emotionally predisposed to interact and learn from these environments in ways that nonhuman apes are not.

The specific role of learning in the development of dog social competence remains an area of active inquiry, and our current findings cannot clearly delineate the contributions of biological and environmental effects on these traits. Although all dogs in this study had substantial experience with humans, dogs with widely varied rearing histories and current living conditions exhibited similar patterns of covariance in skills for cooperative communication. Therefore, while experience with humans may partially account for our findings, these patterns were robust to considerable heterogeneity in the life experiences of our subjects. In conjunction with data showing that puppies as young as 6 weeks of age exhibit sensitivity to a range of cooperative communicative gestures (Riedel et al., 2008), our findings suggest that minimal socialization may be sufficient for the emergence of these patterns. Nevertheless, as in humans, early emerging social skills for cooperative communication likely continue to develop across dog ontogeny (Passalacqua et al., 2011), and these processes may have important consequences for the adult phenotype.

A final alternative explanation for our findings is that dogs solved all social tasks in a similar and relatively inflexible manner. For example, the human experimenter gazed towards the baited location in the point, gaze and reaching conditions, and attention to this feature alone might permit success. Two reasons argue against this interpretation. First, the marker cue did not involve a gazing or pointing element, yet tended to cluster together with the other gestures that did. Second, performance across the four social gestures differed significantly ( $F_{3,1326} = 101.85$ ,  $P < 0.001$ ), and Tukey contrasts revealed significant differences between all conditions with the exception of the reach versus point comparison. Thus, dogs likely used different aspects of social information in each of these tasks.

It is noteworthy that the social similarities we observed between dogs and humans were restricted to measures of cooperative communication, and our exploratory factor analysis with dogs suggests that these skills are not strongly related to other aspects of dog social cognition. For example, measures related to gazing at a human face and discriminating between humans vocalizing with different affect also loaded heavily in this model, but they did not covary strongly with skills for cooperative communication. In contrast, previous analyses across the full test battery used with children confirmed the presence of a factor characterized by diverse social skills, including social learning and theory of mind (Herrmann, Hernandez-Lloreda et al., 2010). Similarly, we found no strong evidence for similarities in physical cognition between

humans and dogs, suggesting that any convergent cognitive structure may be restricted to specific aspects of social cognition.

In addition to their relevance to human cognition, our findings also have implications for the understanding of animal cognition more broadly. Specifically, we found strong evidence that individual differences in dog cognition are best described by multiple factors and are unlikely to be explained by constructs such as general intelligence. This multidimensionality is consistent with previous studies using citizen science data, which also revealed covariance in skills related to gesture comprehension and memory (Stewart et al., 2015). The six factors represented in our data align well with established constructs in cognitive psychology and index processes such as inhibitory control and spatial memory, in addition to processes involved in social cognition. Our main findings are unlikely to be explained by differences between populations, breeds and rearing or training within our sample because we found evidence for similar correlational patterns within each of the three dog populations. Therefore, our main findings are consistent both within and across heterogeneous populations, supporting the hypothesis that these data reflect species-level characteristics.

Finally, it is important to emphasize that while our data reflect a relatively robust phenomenon, we remain limited in our explanations for it. Although our results reveal similar patterns in cooperative communication between dogs and children, these skills may be supported by different cognitive representations in each species (MacLean, Krupenye, & Hare, 2014). Specifically, children's gestural communication is supported by abilities for sharing attention with others and an emerging appreciation of others as intentional agents (Tomasello, Carpenter, & Liszkowski, 2007). Although dogs exhibit flexibility in their communication with humans (Kaminski & Nitzschner, 2013), and may understand some psychological states in others (Bensky, Gosling, & Sinn, 2013), it is likely the two species cognize these interactions in different ways. Notwithstanding these important considerations, the common patterns of individual differences in dogs and humans suggests that dogs may provide an informative and tractable model for questions about key aspects of human behaviour and cognition. For example, research with dogs has already led to powerful insights into the genetic basis of many complex traits and disease processes in humans (Sutter & Ostrander, 2004). Our findings set the stage for similar investigations regarding the sociocognitive skills that are foundational to typical human development (Tomasello, 1999) and disrupted in neurodevelopmental disabilities such as autism (Carpenter, Pennington, & Rogers, 2002). Given that these traits exhibit similar patterns in humans and domestic dogs, but not in chimpanzees, dogs may provide one of the most powerful nonhuman species in which to test hypotheses regarding the evolutionary and developmental basis of these processes, as well as their underlying proximate mechanisms.

## Acknowledgments

We thank K. Rodriguez, K. Almon, S. Laderman, A. Reinhardt, K. Leimberger, K. Duffy, T. Jones, K. Suchman, W. Plautz, L. Strassberg, L. Thielke, E. Blumstein, R. Reddy and K. Cunningham for help with data collection and coding. We thank Canine Companions for Independence and K2 Solutions, Inc. for accommodating research with assistance and detection dogs. We thank J. Russell and W. Hopkins for sharing data from Russell et al. (2011). This research was supported in part by grants from the Office of Naval Research (ONR N00014-12-1-0095), the National Institutes of Health (NIH 5 R03 HD070649-02) and by the AKC Canine Health Foundation. The contents of this publication are solely the responsibility of authors and do not necessarily represent the views of the AKC Canine Health Foundation.

## Supplementary Material

Supplementary Material associated with this article is available, in the online version, at <http://dx.doi.org/10.1016/j.anbehav.2017.01.005>.

## References

- Agnetta, B., Hare, B., & Tomasello, M. (2000). Cues to food location that domestic dogs (*Canis familiaris*) of different ages do and do not use. *Animal Cognition*, 3(2), 107–112.
- Andreeff, M., Ruvolo, V., Gadgil, S., Zeng, C., Coombes, K., Chen, W., et al. (2008). HOX expression patterns identify a common signature for favorable AML. *Leukemia*, 22(11), 2041–2047.
- Batt, L., Batt, M., & McGreevy, P. (2007). Two tests for motor laterality in dogs. *Journal of Veterinary Behavior-Clinical Applications and Research*, 2(2), 47–51.
- 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.
- Branson, N. J., & Rogers, L. J. (2006). Relationship between paw preference strength and noise phobia in *Canis familiaris*. *Journal of Comparative Psychology*, 120(3), 176–183.
- Brauer, J., Call, J., & Tomasello, M. (2005). All great ape species follow gaze to distant locations and around barriers. *Journal of Comparative Psychology*, 119(2), 145–154.
- Brauer, J., Kaminski, J., Riedel, J., Call, J., & Tomasello, M. (2006). Making inferences about the location of hidden food: Social dog, causal ape. *Journal of Comparative Psychology*, 120(1), 38–47.
- Bray, E. E., MacLean, E. L., & Hare, B. A. (2014). Context specificity of inhibitory control in dogs. *Animal Cognition*, 17(1), 15–31. <http://dx.doi.org/10.1007/s10071-013-0633-z>.
- Bray, E. E., MacLean, E. L., & Hare, B. A. (2015). Increasing arousal enhances inhibitory control in calm but not excitable dogs. *Animal Cognition*, 18(6), 1317–1329.
- Budaev, S. (1998). How many dimensions are needed to describe temperament in animals: A factor reanalysis of two data sets. *International Journal of Comparative Psychology*, 11, 17–29.
- Call, J., Brauer, J., Kaminski, J., & Tomasello, M. (2003). Domestic dogs (*Canis familiaris*) are sensitive to the attentional state of humans. *Journal of Comparative Psychology*, 117(3), 257–263.
- Carpenter, M., Nagell, K., & Tomasello, M. (1998). Social cognition, joint attention, and communicative competence from 9 to 15 months of age. *Monographs of the Society for Research in Child Development*, 63(4), 1–143.
- Carpenter, M., Pennington, B. F., & Rogers, S. J. (2002). Interrelations among social-cognitive skills in young children with autism. *Journal of Autism and Developmental Disorders*, 32(2), 91–106.
- Cieri, R. L., Churchill, S. E., Franciscus, R. G., Tan, J., & Hare, B. (2014). Craniofacial feminization, social tolerance, and the origins of behavioral modernity. *Current Anthropology*, 55(4), 419–443.
- de Waal, F. B. M., Boesch, C., Horner, V., & Whiten, A. (2008). Comparing social skills of children and apes. *Science*, 319(5863), 569.
- de Waal, F. B. M., & Tyack, P. L. (2003). *Animal social complexity: Intelligence, culture, and individualized societies*. Cambridge, MA: Harvard University Press.
- Dore, F. Y., Fiset, S., Goulet, S., Dumas, M. C., & Gagnon, S. (1996). Search behavior in cats and dogs: Interspecific differences in working memory and spatial cognition. *Learning & Behavior*, 24(2), 142–149.
- Erdőhegyi, Á., Topál, J., Virányi, Z., & Miklósi, Á. (2007). Dog-logic: Inferential reasoning in a two-way choice task and its restricted use. *Animal Behaviour*, 74, 725–737.
- Fiset, S., Beaulieu, C., & Landry, F. (2003). Duration of dogs' (*Canis familiaris*) working memory in search for disappearing objects. *Animal Cognition*, 6(1), 1–10.
- Fiset, S., Gagnon, S., & Beaulieu, C. (2000). Spatial encoding of hidden objects in dogs (*Canis familiaris*). *Journal of Comparative Psychology*, 114(4), 315.
- Gácsi, M., Györi, B., Virányi, Z., Kubinyi, E., Range, F., Belényi, B., et al. (2009). Explaining dog wolf differences in utilizing human pointing gestures: Selection for synergistic shifts in the development of some social skills. *PLoS One*, 4(8), e6584. <http://dx.doi.org/10.1371/annotation/9d7a0174-3068-4c44-bb98-b8a9bc5a99d5>.
- Gácsi, M., Miklósi, Á., Varga, O., Topál, J., & Csányi, V. (2004). Are readers of our face readers of our minds? Dogs (*Canis familiaris*) show situation-dependent recognition of human's attention. *Animal Cognition*, 7(3), 144–153.
- Goodall, J., Lonsdorf, E. V., Ross, S. R., & Matsuzawa, T. (2010). *The mind of the chimpanzee: Ecological and experimental perspectives*. Chicago, IL: University of Chicago Press.
- Hair, J. F., Anderson, R. E., Tatham, R. L., & Black, W. (1998). *Multivariate data analysis*. Upper Saddle River, NJ: Prentice Hall.
- Hare, B. (2017). Survival of the friendliest: *Homo sapiens* evolved via selection for prosociality. *Annual Review of Psychology*, 68(1), 155–186.
- Hare, B., Brown, M., Williamson, C., & Tomasello, M. (2002). The domestication of social cognition in dogs. *Science*, 298(5598), 1634–1636.
- Hare, B., Call, J., & Tomasello, M. (1998). Communication of food location between human and dog (*Canis familiaris*). *Evolution of Communication*, 2(1), 137–159.
- Hare, B., Plyusnina, I., Ignacio, N., Schepina, O., Stepika, A., Wrangham, R., et al. (2005). Social cognitive evolution in captive foxes is a correlated by-product of experimental domestication. *Current Biology*, 15(3), 226–230.
- Hare, B., & Tomasello, M. (2004). Chimpanzees are more skilful in competitive than in cooperative cognitive tasks. *Animal Behaviour*, 68, 571–581.
- Hare, B., & Tomasello, M. (2005). Human-like social skills in dogs? *Trends in Cognitive Sciences*, 9(9), 439–444.
- Hare, B., Wobber, V., & Wrangham, R. (2012). The self-domestication hypothesis: Evolution of bonobo psychology is due to selection against aggression. *Animal Behaviour*, 83, 573–585.
- Harr, A. L., Gilbert, V. R., & Phillips, K. A. (2009). Do dogs (*Canis familiaris*) show contagious yawning? *Animal Cognition*, 12(6), 833–837.
- Head, E., Callahan, H., Muggenburg, B., Cotman, C., & Milgram, N. (1998). Visual-discrimination learning ability and  $\beta$ -amyloid accumulation in the dog. *Neurobiology of Aging*, 19(5), 415–425.
- Herrmann, E., Call, J., Hernandez-Lloreda, M. V., Hare, B., & Tomasello, M. (2007). Humans have evolved specialized skills of social cognition: The cultural intelligence hypothesis. *Science*, 317(5843), 1360–1366.
- Herrmann, E., Call, J., Hernandez-Lloreda, M. V., Hare, B., & Tomasello, M. (2008). Comparing social skills of children and apes – Response. *Science*, 319(5863), 570.
- Herrmann, E., Hare, B., Call, J., & Tomasello, M. (2010). Differences in the cognitive skills of bonobos and chimpanzees. *PLoS One*, 5(8), e12438. <http://dx.doi.org/10.1371/journal.pone.0012438>.
- Herrmann, E., Hernandez-Lloreda, M. V., Call, J., Hare, B., & Tomasello, M. (2010). The structure of individual differences in the cognitive abilities of children and chimpanzees. *Psychological Science*, 21(1), 102–110.
- Horn, J. L. (1965). A rationale and test for the number of factors in factor analysis. *Psychometrika*, 30(2), 179–185.
- Horn, L., Virányi, Z., Miklósi, Á., Huber, L., & Range, F. (2012). Domestic dogs (*Canis familiaris*) flexibly adjust their human-directed behavior to the actions of their human partners in a problem situation. *Animal Cognition*, 15, 57–71.
- Itakura, S., Agnetta, B., Hare, B., & Tomasello, M. (1999). Chimpanzee use of human and conspecific social cues to locate hidden food. *Developmental Science*, 2(4), 448–456.
- Jakovcovic, A., Elgier, A. M., Mustaca, A. E., & Bentosela, M. (2010). Breed differences in dogs' (*Canis familiaris*) gaze to the human face. *Behavioural Processes*, 84(2), 602–607.
- Joly-Mascheroni, R. M., Senju, A., & Shepherd, A. J. (2008). Dogs catch human yawns. *Biology Letters*, 4(5), 446–448.
- Kaiser, H. F. (1970). A second generation little jiffy. *Psychometrika*, 35(4), 401–415.
- Kaiser, H. F., & Rice, J. (1974). Little Jiffy, Mark IV. *Journal of Educational and Psychological Measurement*, 34(1), 111–117.
- Kaminski, J., Call, J., & Fischer, J. (2004). Word learning in a domestic dog: Evidence for 'fast mapping'. *Science*, 304(5677), 1682–1683.
- Kaminski, J., & Nitzschner, M. (2013). Do dogs get the point? A review of dog-human communication ability. *Learning & Motivation*, 44(4), 294–302.
- Kerr, M. K., & Churchill, G. A. (2001). Bootstrapping cluster analysis: Assessing the reliability of conclusions from microarray experiments. *Proceedings of the National Academy of Sciences of the United States of America*, 98(16), 8961–8965.
- MacLean, E. L., & Hare, B. (2015). Dogs hijack the human bonding pathway. *Science*, 348(6232), 280–281.
- MacLean, E. L., Hare, B., Nunn, C. L., Addessi, E., Amici, F., Anderson, R. C., et al. (2014). The evolution of self-control. *Proceedings of the National Academy of Sciences of the United States of America*, 111(20), E2140–E2148. <http://dx.doi.org/10.1073/pnas.1323533111>.
- MacLean, E. L., Krupenye, C., & Hare, B. (2014b). Dogs (*Canis familiaris*) account for body orientation but not visual barriers when responding to pointing gestures. *Journal of Comparative Psychology*, 128(3), 285–297. <http://dx.doi.org/10.1037/a0035742>.
- Merola, I., Prato-Previde, E., & Marshall-Pescini, S. (2012). Social referencing in dog-owner dyads? *Animal Cognition*, 15, 175–185.
- Miklósi, Á., Kubinyi, E., Topál, J., Gácsi, M., Virányi, Z., & Csányi, V. (2003). A simple reason for a big difference: Wolves do not look back at humans, but dogs do. *Current Biology*, 13(9), 763–766.
- Miklósi, Á., Polgárdi, R., Topál, J., & Csányi, V. (1998). Use of experimenter-given cues in dogs. *Animal Cognition*, 1(2), 113–121.
- Nagasawa, M., Kikusui, T., Onaka, T., & Ohta, M. (2009). Dog's gaze at its owner increases owner's urinary oxytocin during social interaction. *Hormones and Behavior*, 55(3), 434–441.
- O'Hara, S. J., & Reeve, A. V. (2011). A test of the yawning contagion and emotional connectedness hypothesis in dogs, *Canis familiaris*. *Animal Behaviour*, 81, 335–340.
- Osborne, J. W., & Costello, A. B. (2009). Best practices in exploratory factor analysis: Four recommendations for getting the most from your analysis. *Pan-Pacific Management Review*, 12(2), 131–146.
- Osthaus, B., Marlow, D., & Ducat, P. (2010). Minding the gap: Spatial perseveration error in dogs. *Animal Cognition*, 13(6), 881–885.
- Passalacqua, C., Marshall-Pescini, S., Barnard, S., Lakatos, G., Valsecchi, P., & Previde, E. P. (2011). Human-directed gazing behaviour in puppies and adult dogs, *Canis lupus familiaris*. *Animal Behaviour*, 82, 1043–1050.
- Pilley, J. W., & Reid, A. K. (2011). Border collie comprehends object names as verbal referents. *Behavioural Processes*, 86(2), 184–195.
- Pongrácz, P., Miklósi, Á., Kubinyi, E., Gurobi, K., Topál, J., & Csányi, V. (2001). Social learning in dogs: The effect of a human demonstrator on the performance of dogs (*Canis familiaris*) in a detour task. *Animal Behaviour*, 62, 1109–1117.

- R Core Team. (2015). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
- Range, F., Aust, U., Steurer, M., & Huber, L. (2008). Visual categorization of natural stimuli by domestic dogs. *Animal Cognition*, *11*(2), 339–347.
- Riedel, J., Buttelmann, D., Call, J., & Tomasello, M. (2006). Domestic dogs (*Canis familiaris*) use a physical marker to locate hidden food. *Animal Cognition*, *9*(1), 27–35.
- Riedel, J., Schumann, K., Kaminski, J., Call, J., & Tomasello, M. (2008). The early ontogeny of human–dog communication. *Animal Behaviour*, *75*, 1003–1014.
- Rooijackers, E., Kaminski, J., & Call, J. (2009). Comparing dogs and great apes in their ability to visually track object transpositions. *Animal Cognition*, *12*(6), 789–796.
- Russell, J. L., Lyn, H., Schaeffer, J. A., & Hopkins, W. D. (2011). The role of socio-communicative rearing environments in the development of social and physical cognition in apes. *Developmental Science*, *14*(6), 1459–1470.
- Silva, K., Bessa, J., & de Sousa, L. (2012). Auditory contagious yawning in domestic dogs (*Canis familiaris*): First evidence for social modulation. *Animal Cognition*, *15*(4), 721–724.
- Stevens, J. P. (2012). *Applied multivariate statistics for the social sciences*. New York, NY: Routledge.
- Stewart, L., MacLean, E. L., Ivy, D., Woods, V., Cohen, E., Rodriguez, K., et al. (2015). Citizen science as a new tool in dog cognition research. *PLoS One*, *10*(9), e0135176.
- Sutter, N. B., & Ostrander, E. A. (2004). Dog star rising: The canine genetic system. *Nature Reviews Genetics*, *5*(12), 900–910.
- Szetei, V., Miklósi, Á., Topál, J., & Csányi, V. (2003). When dogs seem to lose their nose: An investigation on the use of visual and olfactory cues in communicative context between dog and owner. *Applied Animal Behaviour Science*, *83*(2), 141–152.
- Téglás, E., Gergely, A., Kupán, K., Miklósi, Á., & Topál, J. (2012). Dogs' gaze following is tuned to human communicative signals. *Current Biology*, *22*(3), 209–212.
- Tomasello, M. (1999). *The cultural origins of human cognition*. Cambridge, MA: Harvard University Press.
- Tomasello, M., Carpenter, M., & Liszkowski, U. (2007). A new look at infant pointing. *Child Development*, *78*(3), 705–722.
- Tomkins, L. M., Thomson, P. C., & McGreevy, P. D. (2010). First-stepping test as a measure of motor laterality in dogs (*Canis familiaris*). *Journal of Veterinary Behavior-Clinical Applications and Research*, *5*(5), 247–255.
- Topál, J., Gergely, G., Erdőhegyi, Á., Csibra, G., & Miklósi, Á. (2009). Differential sensitivity to human communication in dogs, wolves, and human infants. *Science*, *325*(5945), 1269–1272.
- Udell, M. A. R., Dorey, N. R., & Wynne, C. D. L. (2010). What did domestication do to dogs? A new account of dogs' sensitivity to human actions. *Biological Reviews of the Cambridge Philosophical Society*, *85*, 327–345.
- Vas, J., Topál, J., Gácsi, M., Miklósi, Á., & Csányi, V. (2005). A friend or an enemy? Dogs' reaction to an unfamiliar person showing behavioural cues of threat and friendliness at different times. *Applied Animal Behaviour Science*, *94*(1–2), 99–115.
- Virányi, Z., Gácsi, M., Kubinyi, E., Topál, J., Belényi, B., Ujfalussy, D., et al. (2008). Comprehension of human pointing gestures in young human-reared wolves (*Canis lupus*) and dogs (*Canis familiaris*). *Animal Cognition*, *11*(3), 373–387.
- West-Eberhard, M. J. (2003). *Developmental plasticity and evolution*. Oxford, U.K.: Oxford University Press.
- Wobber, V., & Hare, B. (2011). Psychological health of orphan bonobos and chimpanzees in African sanctuaries. *PLoS One*, *6*(6), e17147.
- Wobber, V., Herrmann, E., Hare, B., Wrangham, R., & Tomasello, M. (2014). Differences in the early cognitive development of children and great apes. *Developmental Psychobiology*, *56*(3), 547–573.