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Dog cognitive development: A longitudinal study across the first two years of life

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Abstract

While our understanding of adult dog cognition has grown considerably over the past twenty years, relatively little is known about the ontogeny of dog cognition. To assess the development and longitudinal stability of cognitive traits in dogs, we administered a battery of tasks to 160 candidate assistance dogs at two timepoints. The tasks were designed to measure diverse aspects of cognition, ranging from executive function (e.g., inhibitory control, reversal learning, memory) to sensory discrimination (e.g., vision, audition, olfaction) to social interaction with humans. Subjects first participated as 8-to-10-week old puppies, and then were retested on the same tasks at approximately 21 months of age. With few exceptions, task performance improved with age, with

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Conflict of Interest: The authors declare that they have no conflicts of interest.

Declarations

Ethics approval: All testing procedures were reviewed and adhered to regulations set forth by the University of Arizona Institutional Animal Care and Use Committee (IACUC # 16–175) and were collected in accordance with relevant guidelines and regulations.

Data availability: The datasets generated during and analyzed during the current study are available from the corresponding author on reasonable request.

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the largest effects observed for measures of executive function and social gaze. Results also indicated that individual differences were both early emerging and enduring; for example, social attention to humans, use of human communicative signals, independent persistence at a problem, odor discrimination, and inhibitory control all exhibited moderate levels of rank-order stability between the two timepoints. Using multiple regression, we found that young adult performance on many cognitive tasks could be predicted from a set of cognitive measures collected in early development. Our findings contribute to knowledge about changes in dog cognition across early development as well as the origins and developmental stability of individual differences.

Keywords

Assistance dog; behavior; **c**ognition; development; longitudinal; individual differences

Introduction

Ontogeny provides an important window into the nature of any complex trait, as emphasized by Tinbergen (1963) when he dedicated one of his four questions to development. However, studies of animal cognition often focus on the cognitive phenotypes of adult animals, with limited knowledge about their developmental bases (Rosati, Wobber, Hughes, & Santos, 2014). Domestic dogs present rich opportunities for comparative studies of cognitive development given their ubiquity in human societies, employment in diverse working dog applications, and highly variable environments throughout development. Although dog cognition has been extensively studied throughout the last two decades, the majority of studies have focused on adult animals, often aiming to characterize species-typical performance on cognitive tasks, with less emphasis on individual differences or their development (Arden, Bensky, & Adams, 2016; Bensky, Gosling, & Sinn, 2013; MacLean, Herrmann, Suchindran, & Hare, 2017).

One common approach for inferring how variation in developmental experiences affects adult cognition compares adult phenotypes of dogs who have (presumably) experienced different environmental conditions during development. These studies have evaluated both social cognition (i.e. communicative cues, measures of social gaze) and nonsocial cognition (i.e. inhibitory control, independent problem solving, causal inferences), and compared the performance of pet dogs living in homes to other groups with less human contact, including shelter (Duranton & Gaunet, 2016), kennel-housed (Turcsán et al., 2020), purpose-bred research (Lazarowski & Dorman, 2015), pack-raised (Lampe, Bräuer, Kaminski, & Virányi, 2017), and free-ranging (Brubaker, Dasgupta, Bhattacharjee, Bhadra, & Udell, 2017) dogs. Some of these studies find no difference in the cognitive performance of dogs with different rearing histories (Brubaker et al., 2017; Fagnani, Barrera, Carballo, & Bentosela, 2016; Lampe et al., 2017), but others support the conclusion that pet dogs are more adept at using social cues and more persistent at solving problems than dogs living or reared in kennel environments (Duranton & Gaunet, 2016; Lazarowski & Dorman, 2015). While informative with respect to adult phenotypes, these studies lack measures of early-life cognition and thus cannot directly characterize cognitive development.

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Other methods for studying changes across the lifespan involve cross-sectional or longitudinal research. These approaches have been common in studies of canine temperament and personality (e.g., Goddard & Beilharz, 1984b; Head et al., 1997; Jones & Gosling, 2005; Marshall-Pescini, Virányi, Kubinyi, & Range, 2017; Riemer, Müller, Virányi, Huber, & Range, 2016; Scott & Fuller, 1965; Sforzini et al., 2009; Starling, Branson, Thomson, & McGreevy, 2013; Wallis, Szabó, & Kubinyi, 2020), but are less commonly employed in cognitive research. Bensky et al. (2013) reported that of 222 canine cognition studies published through 2012, only 12.6% employed a cross-sectional or longitudinal design. Many of those studies investigated the development of socio-cognitive skills, as have several papers published subsequently (e.g., Bhattacharjee et al., 2017; Gácsi, Györi, et al., 2009; Lazarowski, Rogers, Waggoner, & Katz, 2019; Lazarowski, Strassberg, Waggoner, & Katz, 2019; Rossano, Nitzschner, & Tomasello, 2014; Zaine, Domeniconi, & Wynne, 2015). In contrast, cross-sectional or longitudinal studies of nonsocial cognition have tended to focus on older dogs and cognitive decline associated with aging (e.g., Christie et al., 2005; Head, 2013; Milgram et al., 2002; Milgram, Head, Weiner, & Thomas, 1994; Piotti et al., 2018; Tapp et al., 2003; Wallis et al., 2014; Watowich et al., 2020). Of the few that have investigated the early development of nonsocial cognition, one recent study in a population of working dogs (tested at 3, 6, and 11 months of age) found that inhibitory control, attention, and spatial cognition all improved with age (Lazarowski, Krichbaum, Waggoner, & Katz, 2020). These findings suggest that important cognitive changes are occurring over early development and highlight the need for further research on these processes.

Lastly, one important question about cognitive development—which can only be addressed through a longitudinal design—concerns the stability of individual differences across time. Again, this question has been addressed in numerous studies of canine personality and temperament (e.g., Fratkin, Sinn, Patall, & Gosling, 2013; Goddard & Beilharz, 1984a, 1986; Harvey, Craigon, Blythe, England, & Asher, 2017; Harvey et al., 2016; Riemer et al., 2016; Svartberg, Tapper, Temrin, Radesäter, & Thorman, 2005; Tomkins, Thomson, & McGreevy, 2010; Wilsson & Sundgren, 1998). However, very few cognitive studies have implemented similar longitudinal approaches. Riemer et al. (2014) reported that cognitive impulsivity in 13 dogs, quantified via performance on a delay of gratification task as well as owner assessment on a questionnaire, was highly stable across a six year timespan; on the other hand, they found that a measure of motor impulsivity was not correlated across the two timepoints. Gácsi et al. (2009) conducted a pointing task where a subset of subjects participated at two timepoints: 12 puppies were retested 1 to 12 weeks after the initial test, another 12 puppies were retested 8 to 18 months later (as adults), and 12 adults were retested 1 week to 6 months later. In that study, there were no effects of age on performance and the small sample size precluded a powerful assessment of the developmental stability of individual differences.

The literature reviewed above has either indirectly assessed cognitive development or focused on the development of a limited subset of cognitive traits. We sought to fill these gaps in our understanding by conducting the first large-scale longitudinal study of canine social and nonsocial cognition, allowing us to assess both the early development and stability of a wide range of cognitive traits. Here, we report the results of this multi-year study in which we tracked individual differences in cognition in a population of 160

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candidate assistance dogs. All dogs were whelped and weaned in Northern California and participated in the Dog Cognitive Development Battery (DCDB; Bray et al., 2020) at ~9 weeks of age. This test battery – derived from the dog cognition test battery for adult dogs (MacLean et al., 2017) – was designed with the goal of measuring individual differences across a diverse range of cognitive processes. After completing testing, dogs were then raised in the homes of volunteers throughout the western United States until ~21 months of age, at which point they returned to professional training centers and completed the test battery a second time. We investigated changes in task performance across ontogeny—i.e. how performance changed from ~9 weeks of age to young adulthood—as well as the stability of individual differences across time—i.e. the extent to which task performance as a puppy predicted subsequent performance in young adulthood.

Regarding changes in skills related to age, we hypothesized that for tasks where there was an objectively correct response (e.g., object-choice tasks), cognitive performance would improve from ~9 weeks to ~21 months. We also expected that at least a subset of traits would exhibit consistent individual differences across time, although given the lack of previous research in this area, we had no *a priori* hypotheses regarding the relative stability of different traits.

General Methods

Subjects

All subjects were recruited from Canine Companions for Independence (Santa Rosa, CA, USA), a non-profit assistance dog organization in the United States. Canine Companions granted informed consent to all aspects of the study. All testing procedures were reviewed and adhered to regulations set forth by the Institutional Animal Care and Use Committee at the University of Arizona (IACUC No. 16–175).

We aimed to test all subjects on the same tasks at two different timepoints: first in early development and later in young adulthood. To this end, we tested 168 puppies (97 females and 71 males) from February to July of 2017 at approximately 9 weeks of age (mean = 9.20 weeks, range 7.86 – 10.43 weeks). Our sample included 122 Labrador x golden crosses, 40 Labrador retrievers, and 6 golden retrievers from 65 different litters (Bray et al., 2020). After their initial testing, these dogs were raised by volunteer puppy raisers throughout the western United States for ~18 months before returning to Canine Companions for Independence for professional training. Of the original 168 puppies, we were able to test all but eight individuals as young adults ($n = 5$ released for medical reasons prior to turn-in, $n = 1$ released for behavioral reasons prior to turn-in, $n = 2$ did not meet participation criteria at turn-in). Thus, our final sample consisted of 160 dogs (93 females and 67 males). These dogs were tested for a second time from January 2018 to April 2019 when they were just under two years old (mean = 1.79 years, range 0.99 to 2.01 years), within a month of each dog returning to Canine Companions' Northwest (Santa Rosa, CA) or Southwest (Oceanside, CA) regional campuses for professional training. The dogs who participated in both rounds of testing included 118 Labrador x golden crosses, 37 Labrador retrievers, and 5 golden retrievers.

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Procedure

Dog Cognitive Development Battery (DCDB)—The DCDB (Bray et al., 2020) consists of a series of tasks designed to assess aspects of perception, executive function, communication, social motivation, and temperament (Table S1). All dogs completed this battery once in early development (~9 weeks of age) and again in young adulthood (~1.8 years of age). The general methods used with puppies and adults were identical except for one task that was only presented to adults, as well as minor procedural differences required to obtain age-appropriate measures, described below (e.g., retention intervals on memory tasks).

Implementation with puppies: Puppies completed testing in a dedicated 19.5’ x 14’ room at Canine Companions for Independence’s Canine Early Development Center. Each subject completed one ~45-minute session per day over three consecutive days (Fig. 1a). All of the cognitive tasks in the DCDB are briefly described below; detailed experimental methods and video examples are provided in Bray et al. (2020), as well as in the Supplementary Material. Because the temperament tasks (i.e. novel object and surprising events) were not the focus of the current study, detailed methods for these tasks are not presented here but are available in a separate manuscript (Bray et al., 2020). Although we primarily categorized laterality as a temperament task (Batt, Batt, Baguley, & McGreevy, 2009), we include it here as there is some evidence across species that behavioral lateralization (i.e. handedness) is associated with cognition (Bibost & Brown, 2014; Güntürkün, Ströckens, & Ocklenburg, 2020; Magat & Brown, 2009; although see Whiteside et al., 2020). However, given that measures of behavioral lateralization have been shown to vary based on the task in humans (Annett, 1994) and dogs (e.g., Batt, Batt, Baguley, & McGreevy, 2008; Tomkins et al., 2010; Wells, 2003), it is a limitation of the current study that we only include only one measure of laterality. Nonetheless, the measure of laterality that we included has been associated with measures of both structural and sensory laterality and is among the most widely-used assessments of laterality in dogs (Tomkins, Williams, Thomson, & McGreevy, 2012).

For the sake of comparison between individuals, all subjects completed the tasks in the same order (Bray, Sammel, Seyfarth, Serpell, & Cheney, 2017; MacLean et al., 2017). For tasks requiring a choice (e.g., hiding-finding warm-ups, cylinder, gesture use, working memory, and perceptual discriminations), if a puppy did not choose within the predetermined number of seconds or if there was an experimenter error, that trial was repeated. If the subject’s lack of interest in participation continued, we employed a standardized protocol for trying to re-engage and refamiliarize the puppy with the task and if necessary gave the puppy a break before returning to the task (see the Supplementary Material and Bray et al. (2020) for specific refamiliarization and abort criteria for each task). On infrequent occasions, when those attempts were ineffective, and as indicated by the predetermined abort criteria, the task was discontinued for that puppy (Supplementary Table S2).

Vision pretest –: This test ensured that puppies were capable of tracking visual stimuli at the typical distances used in subsequent tasks (based on Ollivier, Plummer, & Barrie, 2007). At a distance of 100 cm in front of the puppy, a cotton ball was dropped vertically and flicked across the ground in full view of the subject. Subjects were required to follow the motion of

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the cotton ball on at least three trials to advance to subsequent tasks. All puppies tested met this criterion.

Retrieval (Fig. 1a task 1, Fig. 1b task 1) –: This task measured the puppy's willingness to cooperatively engage in fetch with a human partner (based on Bray, Sammel, Seyfarth, et al., 2017; Slabbert & Odendaal, 1999; Wilsson & Sundgren, 1997). Following a 1 min familiarization period (see Supplementary Material), the experimenter threw a small ball for the puppy and vocally encouraged the dog to bring the ball back to her. For each of the two 1 min test trials, the puppy received a score based on the following scoring system: (1) did not interact with the ball at all, (2) only chased the ball, (3) also picked the ball up in the mouth, (4) returned the ball to the experimenter one to two times, or (5) returned the ball to the experimenter three or more times. The dependent measures were the puppy's average score across two trials and a tally of the total number of times that the puppy returned the ball to the experimenter.

Laterality (Fig. 1a task 2, Fig. 1b task 2) –: This task indexed behavioral measures of laterality by tracking the puppy's paw preference when stepping onto and off of a platform (based on Tomkins et al., 2010), which is believed to reflect lateralization in the brain and has been previously linked to temperamental reactivity in adult dogs (Branson & Rogers, 2006). Following a brief introduction to the platform (see Supplementary Material), puppies were held by the handler and then called by the experimenter to step onto the platform across a series of 15 trials, and then off the platform across a series of 15 trials. The forelimb used to initiate this motion on each trial was recorded and subsequently used to compute a laterality index.

Hiding-finding warm-ups –: Warm-up trials ensured that puppies were motivated to search for the reward and capable of reliably choosing between two options in an object choice paradigm. After an initial familiarization to the apparatus and choice procedure (see Supplementary Material), two opaque containers were placed in front of the puppy. In this task and subsequent object choice tasks (i.e. gesture use and working memory), a piece of kibble was taped to the inside bottom of both containers as a control for odor cues. The experimenter showed the puppy a food reward and placed it underneath one of the containers. Puppies were required to choose correctly by physically touching the baited container with snout or front paw on four of five consecutive trials to advance to subsequent object choice tasks. Puppies completed this task once per session.

Human interest (Fig. 1a task 3, Fig. 1b task 3) –: This task measured the puppy's motivation to attend to a human who spoke to the puppy using dog-directed speech (Ben-Aderet, Gallego-Abenza, Reby, & Mathevon, 2017; Gergely, Faragó, Galambos, & Topál, 2017). The experimenter stood outside the testing pen, looked at the puppy, and recited a predetermined script with a fluctuating, high-pitched intonation (Ben-Aderet et al., 2017). After each recitation, the experimenter entered the pen and petted the puppy if approached. This procedure was repeated three times. The duration of the puppy's gaze to the human's face during the recitation of the script and the duration of interaction with the experimenter during play breaks was recorded across trials.

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Cylinder inhibitory control and Cylinder reversal learning (Fig. 1a task 4, Fig. 1b task 4) –: The first part of this task measured the puppy's inhibitory control (i.e. the ability to suppress a prepotent response in favor of a choice that would ultimately be more productive) by requiring the puppy to detour to the reward location, thereby placing distance between herself and a visible reward (based on Bray, MacLean, & Hare, 2014; MacLean et al., 2014). This task is often employed in the canine literature as a measure of motor inhibition (Brucks, Marshall-Pescini, Wallis, Huber, & Range, 2017; Fagnani et al., 2016; Marshall-Pescini, Virányi, & Range, 2015; but for critiques see Kabadyi, Bobrowicz, & Osvath, 2018; van Horik et al., 2018; van Horik, Beardsworth, Laker, Whiteside, & Madden, 2020). The second part of this task measured the puppy's ability to exhibit cognitive flexibility when the demands of the task changed, and the puppy's previously preferred solution was no longer available. Puppies first participated in familiarization trials by walking around the front of an opaque cylinder to retrieve a reward from one of the side openings. In a) inhibitory control test trials, a transparent cylinder was used such that subjects had to resist the prepotent response to move directly towards the visible food, instead avoiding the transparent obstacle. Eight trials were conducted. The dependent measures were the proportion of trials that the puppy successfully retrieved the food from either side opening of the cylinder, without first touching the exterior of the apparatus, and the average latency to obtain the reward. In b) reversal learning test trials, the puppy's preferred side entrance to the cylinder was obstructed by a transparent plastic barrier and subjects were required to switch their response, detouring to the other opening of the apparatus to retrieve the treat. Eight test trials were conducted. The dependent measure was the proportion of trials that puppies performed the correct detour response without first touching the barrier or exterior of the cylinder. The side of the apparatus that the subject first approached (i.e. open or blocked) and the average latency to obtain the reward were also recorded as measures of response flexibility.

Unsolvable (Fig. 1a task 5, Fig. 1b task 9) –: This task measured the puppy's inclination to persist at an unsolvable task independently versus looking at a nearby human experimenter, potentially to solicit help (based on Miklósi et al., 2003; for alternative explanations of what this task measures see Lazzaroni et al., 2020). The puppy was familiarized with displacing the lid from a transparent container to obtain a visible food reward inside. Then, across four 30 s test trials, the lid to the container was affixed, and the dependent measures were the duration of time gazing at the experimenter's face and duration of time physically manipulating the container.

Gesture use –: The experimenter showed the puppy a food reward, then used a foamboard occluder to block the puppy's view while placing the reward inside one of two possible hiding locations. The experimenter then removed the occluder, provided one of three cues (communicative marker, arm pointing, odor control; see below) before subjects could search and recorded the subject's first choice.

Communicative marker **(**Fig. 1a **task 6,** Fig. 1b **task 5)** –

This task measured the puppy's ability to use an arbitrary marker, used in a communicative manner, to find a hidden reward (based on Agnetta, Hare, & Tomasello, 2000; Riedel, Buttelmann, Call, & Tomasello, 2006). The experimenter

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ostensively (preceded by verbally addressing and making eye contact with the puppy) placed a small yellow block that the puppy had never seen before next to the baited location. Twelve test trials were conducted.

Arm pointing **(**Fig. 1a **task 7,** Fig. 1b **task 6)** –

This task measured the puppy's ability to use an arm-pointing gesture to find a hidden reward (based on Hare, Call, & Tomasello, 1998; Miklósi, Polgárdi, Topál, & Csányi, 1998). The experimenter ostensively (preceded by verbally addressing and making eye contact with the puppy) pointed with the contralateral arm, index finger extended, and gazed towards the baited location until the trial ended. Twelve test trials were conducted.

Odor control **(**Fig. 1a **task 8,** Fig. 1b **task 7)** –

This task acted as a control to ensure that puppies' performance on the gesture use tasks could not be attributed to olfactory cues or unintentional cuing by the experimenter (based on Bräuer, Kaminski, Riedel, Call, & Tomasello, 2006; Hare, Brown, Williamson, & Tomasello, 2002; Miklósi et al., 1998). After baiting, the experimenter remained still and did not provide any social information. Eight test trials were conducted.

The dependent measures for the gesture-use tasks were the proportion of trials that the puppy's first choice was to the baited location, where a choice was defined as the puppy physically touching the cup with the snout or a front paw (see Supplementary Material).

Working memory (Fig. 1a task 10, Fig. 1b task 10) –: This task measured the puppy's ability to recall the location of a hidden treat after temporal delays of various lengths (based on Doré, Fiset, Goulet, Dumas, & Gagnon, 1996; Fiset, Beaulieu, & Landry, 2003). It was identical to hiding-finding warm-ups with the exception that we imposed a delay before the subject was allowed to search, which increased across blocks of six trials each (5 s, 10 s, 15 s, 20 s). Only individuals who chose correctly on at least four of six trials at 10 s moved on to delays of 15 s, and only those who chose correctly on at least four of six trials at 15 s moved on to delays of 20 s. The proportion of trials that the subject first searched in the baited location was used as the dependent measure.

Perceptual discriminations –: The subject had to choose between two search locations based on a perceptual cue (visual, auditory, olfactory; see below) regarding which location contained the reward.

Visual discrimination **(**Fig. 1a **task 11,** Fig. 1b **task 12)** –

This task measured the puppy's ability to choose a baited location versus an unbaited location based on visual cues. One plate contained five pieces of visible kibble and the other was empty. The experimenter presented the plates directly in front of the puppy before pulling them backward to 50 cm in front of the puppy, equidistant to the left and right sides. Eight test trials were conducted. The proportion of trials that the puppy first approached the baited plate (i.e. the puppy's snout extended over the plate) was used as the dependent measure.

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Auditory discrimination **(**Fig. 1a **task 12,** Fig. 1b **task 13)** –

This task measured the puppy's ability to choose a baited location versus an unbaited location based on auditory cues (based on Bräuer et al., 2006). Two metal bowls, placed approximately 50 cm away from the puppy, were used as the hiding locations. The experimenter sequentially placed her hand into each container, audibly dropping the food into only one of the containers. Eight test trials were conducted. The dependent measure was the proportion of trials that the subject's first search was to the baited location.

Odor discrimination **(**Fig. 1a **task 13,** Fig. 1b **task 14)** –

This task measured the puppy's ability to choose a baited location versus an unbaited location based on olfactory cues. Two sections of rubber tubing with a 90° bend ("elbows") were presented, one of which contained 10 pieces of dry kibble. The ends of the elbows were filled with cotton to prevent the contents from being visible or audible. The experimenter allowed the subject to sniff the opening of each elbow individually for 3 s, and then the elbows were presented side by side for an additional 3 s before being pulled backward 50 cm in front of the puppy, equidistant to the left and right sides. Puppies were released and allowed to move freely for 20 s. On each trial, the first and last elbow that the subject approached was recorded, as well as the cumulative time spent within a marked 10 cm radius around the elbows. Eight test trials were conducted. The dependent measures were the proportion of trials that the subject's first and last responses were directed to the baited location, as well as the proportion of time that the puppy spent within each of the marked radii around the elbows.

This task-by-task description of the DCDB is reprinted from Animal Behaviour, 166, Bray EE, Gruen ME, Gnanadesikan GE, Horschler DJ, Levy KM, Kennedy BS, Hare BA, MacLean EL, Cognitive characteristics of 8- to 10-week-old assistance dog puppies, 193–206, Copyright (2020), with permission from Elsevier.

Implementation with young adults: The adult version of the DCDB was identical to the battery implemented with puppies, apart from the minor changes described below and detailed in the Supplementary Material (Fig. 1b). Adult dogs were tested at Canine Companions campuses in either Santa Rosa, CA (n = 92) or Oceanside, CA (n = 68) within approximately one month of returning for professional training (minimum = 7 days, maximum = 52 days, average = 23 days). All subjects had previously completed the DCDB as puppies. On the rare occasions where adults lacked motivation to participate on a given task, the same protocols and abort criteria used for the puppies were applied (Supplementary Table S3).

1) Removal of vision pretest

a. Because the adult dogs had been selected to enter professional training, their eyes were thoroughly assessed by a veterinary opthamologist and their vision was deemed adequate. We therefore removed the vision pre-test for adult subjects.

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2) *Addition of a physical problem-solving task linked to success in guide dogs* (Fig. 1b task 11)

a. We added an independent problem-solving task that has been associated with training outcomes in a population of guide dogs (Bray, Sammel, Cheney, Serpell, & Seyfarth, 2017). In this task, the dog was required to complete a series of familiarization trials to ensure they were sufficiently motivated and able to meet the physical (motoric) demands of the task. In subsequent test trials, the dog was required to watch and remember where a treat was hidden within several possible locations on an apparatus, and then manipulate the apparatus appropriately to successfully retrieve the food (see Supplementary Material). The dependent measures for this task are shown in Supplementary Table S4. Although dogs did not participate in this task as puppies, we include it here as an outcome variable for Lasso regression models predicting adult performance as a function of multiple phenotypic measures collected from puppies (see below).

3) Minor age-appropriate modifications

a. We increased the difficulty of the working memory task. Adult subjects were required to remember where a treat was hidden while accounting for more possible hiding locations (four vs. two) across longer delays (up to 40 s). Given the long trial times, this was the only task in the battery where if a dog failed to make a choice within the allotted 30 seconds, the next trial was administered rather than repeating the trial.

b. Where needed, larger stimuli were used (e.g., the ball during the retrieval task, the platform during the laterality task, the container during the unsolvable task).

c. Puppies were not yet leash-trained, and thus were held in place at the start line by their collar or shoulders prior to the experimenter giving the release command. In contrast, all adults were leash-trained and thus were held in place at the start line by a short traffic lead that could subsequently be dropped upon the experimenter giving the release command. For the laterality task, the handler stood to the side of the dog (versus straddling the dog) to allow the dog a full range of motion. The side that the handler stood on was counterbalanced across trials. Therefore, all adults participated in 16 (versus 15) “up” and “down” trials so that the handler could stand an equal number of times on the left and right sides.

d. After piloting the odor discrimination task with adult dogs, we determined that the three x 3 s presentations of elbows for dogs to sniff before each test trial (as implemented in the puppy battery) was frustrating and aversive to many subjects, and that adults were sufficiently motivated to participate in test trials after a single initial 3 s presentation of both elbows. Thus, the task was modified such that adults were given the final 3 s presentation only (in which both elbows were simultaneously presented) at the start of each of the six test trials.

e. With the puppies, the battery consisted of three sessions over three days (Fig. 1a). Due to the increased attention span and food motivation of adult dogs, the

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adult version of the DCDB was implemented in two sessions lasting around 1 to 1.5 hours each, either on the same day with a break in between or across two different days (Fig. 1b).

Scoring and statistical analysis

All statistical analyses were carried out in R v.3.6.0 (R Development Core Team, 2016). Most behavioral variables were scored live, but all tasks were videorecorded for reliability assessment and additional analyses. The following measures were later coded from video: select variables from cylinder (latency during inhibitory control and reversal learning trials and first side correct during reversal learning trials), unsolvable (average time manipulating object), and odor discrimination (time at right and left elbow, from which the variables time in proximity to baited option and time in proximity to nonbaited option were subsequently calculated).

For the live-coded data, independent coders scored from video all trials for 20% of randomly selected subjects, and interrater reliability was calculated using Pearson correlation for continuous variables and Cohen's Kappa for categorical variables. For the measures that were not possible to score live, two coders independently scored data from video. The primary coder scored all data for analysis, and a reliability coder scored all trials for 20% of randomly selected subjects.

All measures were reliable for data collected at both timepoints. For the puppy measures, there was high inter-rater agreement on both live-coded (Cohen's kappa: mean = 0.94; Pearson's *r*: mean = 0.96) and video-coded (Cohen's kappa: mean = 0.93; Pearson's *r*: mean = 0.97) measures. Raw reliability statistics for the puppy data are reported in Bray et al. (2020). Reliability was also excellent for adult measures with high inter-rater agreement on live-coded (Cohen's kappa: mean = 0.96; Pearson's *r*: mean = 0.97) and video-coded (Cohen's kappa: mean = 0.99; Pearson's *r*: mean = 0.93) measures. Raw reliability statistics for testing at this second time point are presented in Supplementary Tables S5 and S6.

To assess changes across ontogeny, we conducted paired sample t-tests on DCDB measures collected from dogs at ~9 weeks of age, and again in young adulthood (~18–24 months). To quantify the effect of age at testing on each trait, we calculated Cohen's *d* using the R package "effsize" (Torchiano, 2020), with the 'paired' argument set to true and the 'within' argument set to false. To assess longitudinal stability of traits measured by the DCDB, we used two analytical approaches. First, following traditional approaches for assessing the consistency of individual differences across time, we performed rank-order stability analyses by assessing the Spearman correlation between phenotypes at the two timepoints (Caspi, Roberts, & Shiner, 2005). To test the directional prediction that phenotypes at timepoint 1 would be positively related to phenotypes at timepoint 2, we used a directional hypothesis testing framework, following the conventions ($\delta = 0.01$, $\Upsilon = 0.04$) recommended by Rice & Gaines (1994). Second, we fit Bayesian linear mixed-models (Stan Development Team, 2018) to assess the relationship between phenotypes at timepoint 1 and timepoint 2, controlling for breed, sex, (adult) testing location, and relatedness between individuals, using the "rutilstimeflutre" and "rstan" R packages (Flutre, 2020; Stan Development Team, 2018). For these models, we converted phenotypic measures to z-scores to facilitate

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interpretation and comparison of beta coefficients. Models were fit using four independent MCMC chains with weakly informative Cauchy priors for the beta coefficients relating phenotypes at timepoint 1 to phenotypes at timepoint 2. Each chain employed a 5,000-iteration burn-in period followed by 15,000 iterations of sampling, using a 25-sample thinning interval. The results across chains were merged to obtain the final posterior distributions.

In addition to modeling the stability of individual DCDB measures across time, we also conducted exploratory analyses using multiple phenotypic measures collected from puppies as predictors of each single adult measure. Thus, rather than focusing on stability in a single given measure across time, these analyses investigated whether any of the phenotypic measures collected from puppies predicted variance in adult phenotypes. For tasks with multiple dependent measures, we first used principal components analysis (PCA) to reduce the number of variables associated with each task (performed separately for puppies and adults). The collective set of variables associated with each task was converted to z-scores prior to parallel analysis (Horn, 1965) using the R package “psych” (Revelle, 2019) to determine the number of components to retain. If parallel analysis suggested retention of zero components for a task, we retained the original dependent measures without performing PCA. In all other cases we performed PCA and extracted the recommended number of components using a varimax rotation to facilitate interpretation of component loadings. The one exception was the laterality task, for which we also retained the original dependent measures without performing PCA, due to evidence in the literature that both bias strength (Barnard, Wells, Hepper, & Milligan, 2017; Branson & Rogers, 2006) and directionality (Tomkins, Thomson, & McGreevy, 2012; Wells, Hepper, Milligan, & Barnard, 2017) can be important, depending on the associations being tested.

We next used Lasso regression, implemented in the R package “glmnet” (Friedman, Hastie, & Tibshirani, 2009), for variable selection given the high ratio of variables to observations in our dataset. Lasso regression imposes a penalty (λ) on the beta coefficients, favoring sparse models by shrinking many beta coefficients to zero (Friedman, Hastie, & Tibshirani, 2010). To determine the optimal value for λ in these analyses, we used leave-one-out cross validation to obtain the λ value that yielded the minimum cross-validated error. Lasso models were fit using 14 DCDB measures from puppies (Table 1) as well as breed, sex, coat color, and adult testing location as predictors for each adult outcome measure (Table 2). Finally, we fit unrestricted linear models using the subset of variables with non-zero beta coefficients in the Lasso models (Hastie, Tibshirani, Friedman, & Franklin, 2005; Hastie, Tibshirani, & Wainwright, 2015).

A summary of the primary analyses and their aims is provided in Table 3.

Results and Discussion

Development of cognitive traits: changes across ontogeny

The results from paired-sample t-tests are shown in Table 4, along with the puppy and adult means and effect sizes with 95% confidence intervals. Performance on the majority of measures improved with age (Table 4). Some of the largest increases were in measures of

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executive function: adults substantially outperformed puppies in the cylinder trials involving inhibitory control ($d = 0.78$) and reversal learning (reversal score $d = 0.92$; first side correct $d = 0.80$). There was also large changes in some of the behaviors involving communication and social motivation: the amount of looking to a human in various contexts dramatically increased from early ontogeny to young adulthood (human interest: avg look time $d = 1.14$; unsolvable: avg time looking at human $d = 0.62$), and adults were more skilled at using the marker cue ($d = 0.66$).

However, there were also a handful of tasks in which dogs performed no differently in early ontogeny compared to young adulthood (Table 4). In the laterality task, the mean laterality bias (which incorporates directionality and is reflected by the laterality index) did not differ between the two timepoints, but the strength of this bias significantly increased with age. Additionally, no differences were observed between the two age groups on the visual discrimination task or on two measures from the odor discrimination task—final choice and time spent in proximity to the baited option—suggesting that the requisite sensory and discriminative capabilities reached adult-like states within the first two months of life. Also, in two social referencing tasks, while time spent looking to the experimenter's face significantly increased from early ontogeny to young adulthood (human interest mean ± SD_{puppy} = 6.44 ± 4.00; human interest mean ± SD_{adult} = 15.55 ± 7.31; $t_{141} = 13.62$, $p < 0.001$; unsolvable mean ± SD_{puppy} = 0.98 ± 1.03; unsolvable mean ± SD_{adult} = 3.33 ± 3.62; $t_{158} = 7.79$, $p < 0.001$), there were no significant differences in time spent near the experimenter during the play break period of the human interest task or time spent manipulating the container in the unsolvable task. In the cylinder reversal learning trials, adults showed significant improvement on two measures (reversal score and first side correct), but there was no difference between age groups in the latency to solve the reversal trials. Lastly, there was also no difference between age groups in performance on the odor control trials, with both groups performing at chance expectation (mean ± SD_{puppy} = 49.92 ± 15.64; mean ± SD_{adult} = 50.70 ± 15.88; $t_{154} = 0.42$, $p = 0.68$).

Stability of cognitive traits: early life predictors of adult phenotypes

Longitudinal stability.—We first assessed longitudinal stability of cognitive traits by analyzing the one-to-one correspondence between measures at the two developmental timepoints. The main results from these analyses are shown in Fig. 2.

Across traits, rank-order stability analyses yielded Spearman correlations ranging from −0.07 to 0.19 (Fig. 2). Sixteen of the correlation coefficients were positive, and only six were negative. A one-sample t-test on the rank-order correlation coefficients indicated that the mean correlation coefficient was significantly greater than zero (mean ± SE = 0.06 ± 0.02, $t_{21} = 3.42$, $p < 0.01$), suggesting overall positive relationships between the same traits measured at the two timepoints. Five individual traits had significant rank-order correlations, all of which were positive (Fig. 3). These traits included a measure of attention to a human face during communication (human interest: average looking time, $r_s = 0.19$, $p = 0.02$), independent persistence during an unsolvable task (unsolvable task: average time manipulating box, $r_s = 0.17$, $p = 0.02$), performance in the reversal phase of the cylinder task (cylinder: reversal score, $r_s = 0.16$, $p = 0.03$), accuracy in detecting a baited location via odor

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(odor discrimination: final choice, $r_s = 0.15$, $p = 0.04$), and sensitivity to human communication using an arbitrary cue (communicative marker, $r_s = 0.15$, $p = 0.04$).

The results from Bayesian linear mixed models controlling for breed, sex, testing location, and relatedness between individuals supported similar conclusions. The mean beta coefficients from the posterior distributions for puppy phenotype as a predictor of adult phenotype ranged between −0.09 and 0.16 (Fig. 2). Fifteen of these beta coefficients were positive, and seven were negative. A one-sample t-test indicated that the mean of these beta coefficients was significantly greater than 0 (mean ± SE = 0.05 ± 0.02, $t_{21} = 3.19$, $p < 0.01$). For four measures with positive associations between the puppy and adult phenotypes (cylinder: reversal score, odor discrimination: final choice, communicative marker, and cylinder: latency (reversal trials)), the 90% credible interval (Kruschke, 2014) for the beta coefficient did not contain zero, indicating a credible positive relationship between these puppy and adult phenotypes. Therefore, while individual phenotypes changed substantially across development, for a subset of traits involving interest in and communication with humans, as well as persistence, reversal learning, and odor discrimination, individual differences in puppies were modestly predictive of adult phenotypes (Fig. 2).

Lasso regression models.—We next used a multiple regression approach to identify a set of phenotypic measures collected from puppies that were associated with adult performance on DCDB tasks. For this analysis we excluded all variables from Problem Solving B, because a large percentage (17%) of subjects were unable to pass familiarization trials and thus did not have data for test trials. For the remaining tasks, all of which had many fewer missing observations (mean ± SE_{puppy} = 1.88 ± 0.01%; mean ± SE_{adult} = 1.45 ± 0.01%), missing data were imputed using a k-nearest neighbors approach.

The results of Lasso regressions using puppy phenotypic measures to predict adult phenotypes are shown in Table 5. As described above, the predictor variables for these models were obtained by performing PCA on each puppy task with multiple measures as well as converting all remaining measures to z-scores (Table 1), and the outcome variables for these models were obtained by following this same procedure for the adult tasks (Table 2). For 9 of 15 models, all beta coefficients were shrunk to zero, leaving an intercept only model (data not shown). However, models for the remaining six adult measures all retained some puppy phenotypic measures as predictor variables. Unconstrained linear models using these predictor variables revealed several plausible associations. First, adult performance in the human interest task was positively predicted by puppy performance on the arm pointing, retrieval, and short-term memory tasks. Given that the outcome and two of the three predictor variables all involve communication and dyadic interaction with humans, this result may capture a developmentally stable suite of traits involving cooperative interaction with humans. Second, for the cylinder task, adult performance on the reversal learning trials was positively predicted by puppy performance on the inhibitory control trials and negatively predicted by a slow latency to solve both the inhibitory control and reversal learning trials as a puppy. Third, adult performance on the inhibitory control trials of the cylinder task was positively predicted by puppy performance on the short-term memory task and by a right-paw preference on the laterality task. Given the positive relationships between variables involving impulse control and working memory, the latter two models may reflect

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developmental stability in traits related to executive function. Furthermore, the association between early paw preference and later impulsivity is intriguing and parallels findings in the human literature, in which left-handed people are more likely to show impairments in impulsivity and hyperactivity (e.g., Reid & Norvilitis, 2000; Schmidt, Carvaho, & Simoes, 2017; Shaw & Brown, 1991; Simoes, Carvalho, & Schmidt, 2017).

General Discussion

We tested a sample of candidate assistance dogs (n = 160) at two timepoints on a series of tasks that measured diverse aspects of cognition to explore the early development and stability of individual differences in cognitive traits. Over the developmental period that we investigated (approximately 9 weeks to 21 months), performance on most cognitive tests exhibited age-related improvement. For example, performance on tasks involving executive function (e.g., memory, impulse control, reversal learning) and social motivation (e.g., retrieval, looking toward humans, using communicative cues) all improved with age, a finding that is largely consistent with the few previously published studies exploring the early development of dog cognition (Dorey, Udell, & Wynne, 2010; Lazarowski et al., 2020; Passalacqua et al., 2011; Watowich et al., 2020; Wynne, Udell, & Lord, 2008; but see also Hare et al., 2002; Riedel et al., 2008 & Gàcsi et al., 2009). Particularly large effects were observed on inhibitory control and reversal learning trials of the cylinder task and looking time during the human interest task. On the other hand, there were a handful of cognitive measures on which puppy performance was indistinguishable from adult performance, including persistence at an unsolvable task, time interacting with the human during play breaks in the human interest task, direction of paw preference, performance on the visual discrimination task, time spent near the baited option during the odor discrimination task, and performance on the odor control task (at chance for both age groups).

The findings from this study contribute to the debate in the literature about the evolution of social skills in dogs. In line with several prior studies (Agnetta et al., 2000; Gácsi, Györi, et al., 2009; Gácsi, Kara, et al., 2009; Hare et al., 2002; Kaminski, Schulz, & Tomasello, 2012; Riedel et al., 2008; Rossano et al., 2014; Virányi et al., 2008), our data suggest that dogs are attuned to human communicative gestures from early in development, prior to extensive exposure to humans, as they reliably follow both conventional and novel gestures to find a food reward at above chance levels (while failing to do so in the absence of any social cues). We also find that these abilities improve over time, with adult dogs exhibiting small (arm pointing: *Cohen's d* = 0.30) to medium (communicative marker: *Cohen's d* = 0.66) increases in gesture following ability. The current study design precludes us from determining the extent to which this improvement results from simple maturational processes versus specific environmental experiences. Finally, we also find evidence that individual differences on these measures exhibit some stability across development. Therefore, while absolute ability tends to increase across ontogeny, relative ability between individual dogs is correlated in early development and young adulthood.

The longitudinal nature of our study allowed us to investigate the stability of individual differences across development. We found that some cognitive measures – including propensity to retrieve, auditory discrimination, and interaction time during human interest –

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showed marked interindividual change over development. Conversely, several other cognitive measures – including social gaze toward humans, use of human communicative signals, independent persistence at a problem, odor discrimination, and inhibitory control – exhibit significant rank-order stability across development, suggesting an early emerging and relatively stable pattern of individual differences (Fig. 3). Further, we found evidence that for some traits – including human interest, auditory discrimination, independent problem solving, inhibitory control, and reversal learning – adult phenotypes can be predicted by leveraging multiple predictor variables collected from puppies.

Performance on the reversal learning trials of the cylinder task, which requires inhibition of a previously rewarded behavior and is therefore a measure of impulsivity (Izquierdo & Jentsch, 2012), had one of the highest rank-order correlations between early development and young adulthood. Furthermore, in our Lasso regression models, adult reversal learning scores were predicted by multiple measures related to inhibitory control in early development. These results are consistent with reports in the human literature. For example, the Dunedin Multidisciplinary Health and Development Study, a longitudinal study that followed a cohort of 1,000 children in New Zealand, also found that self-control, measured via questions pertaining to impulsivity, hyperactivity, and inattention, was moderately stable from childhood to young adulthood ($r = 0.30$, $p \leq 0.001$) (Moffitt et al., 2011).

Although this study was conducted in a population of prospective working dogs, if these findings hold across other populations, they have the potential to inform human-animal interactions by facilitating the prediction of adult dog characteristics. Conversely, this research also indicates that there are certain traits for which such prediction would likely be futile. Past studies have documented how features of the dog, including behavior, can affect the human-animal relationship (Curb, Abramson, Grice, & Kennison, 2013; Duffy, Kruger, & Serpell, 2014; Hsu & Serpell, 2003). Thus, on a practical level, having an objective tool through which to screen behavior at the age around which adoption usually occurs, coupled with the emerging knowledge of which behaviors are stable over time, could be extremely useful in enabling responsible and successful pet adoptions.

From an applied perspective, understanding the developmental course of cognition and temperament will be crucial to more efficient selection of assistance dogs. Studies are beginning to document not only the functional impacts (e.g. increasing independence; Hall, MacMichael, Turner, & Mills, 2017) but also the psychosocial benefits (O'Haire & Rodriguez, 2018; Rodriguez, Bryce, Granger, & O'Haire, 2018; Rodriguez, LaFollette, Hediger, Ogata, & O'Haire, 2020) that these highly-trained dogs provide to their handlers. However, most candidate assistance dogs, even among populations specifically bred for these roles, are ultimately released from training programs due to behaviors incompatible with their working role (Bray et al., 2019). Thus, our findings speak to the possibility of screening for relevant characteristics early in a dog's life, and we identify a subset of traits for which this approach may be most profitably employed. It is particularly promising that adult skills in the realms of dyadic communication and executive function can be predicted by puppy performance on these tasks since they are likely to directly impact the human-animal bond, a key component of any assistance dog team (Burrows, Adams, & Spiers, 2008; LaFollette, Rodriguez, Ogata, & O'Haire, 2019). In fact, previous research has linked

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individual differences on similar measures to working dog success (Bray, Sammel, Cheney, et al., 2017; Lazarowski et al., 2020; MacLean & Hare, 2018). Furthermore, individual differences on these measures presumably arise in part due to genetic mechanisms, and future work will benefit from characterizing the heritability and molecular bases of these traits. Thus, in addition to contributing to our knowledge of the ontogeny of canine cognition, our findings may also help guide the processes of screening, selecting, and breeding working dogs in the future.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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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. Anim Cogn, 3(2), 107–112. doi:10.1007/s100710000070

Annett M (1994). Handedness as a continuous variable with dextral shift: sex, generation, and family handedness in subgroups of left-and right-handers. Behavior genetics, 24(1), 51–63. [PubMed: 8192620]

Arden R, Bensky MK, & Adams MJ (2016). A Review of Cognitive Abilities in Dogs, 1911 Through 2016 More Individual Differences, Please! Curr Dir Psychol Sci, 25(5), 307–312. doi:10.1177/0963721416667718

Barnard S, Wells DL, Hepper PG, & Milligan AD (2017). Association between lateral bias and personality traits in the domestic dog (Canis familiaris). J Comp Psychol, 131(3), 246–256. doi:10.1037/com0000074 [PubMed: 28414470]

Batt LS, Batt M, Baguley J, & McGreevy P (2008). Stability of motor lateralisation in maturing dogs. Laterality, 13(5), 468. [PubMed: 18686162]

Batt LS, Batt MS, Baguley JA, & McGreevy PD (2009). The relationships between motor lateralization, salivary cortisol concentrations and behavior in dogs. J Vet Behav, 4(6), 216–222. doi:10.1016/j.jveb.2009.02.001

Ben-Aderet T, Gallego-Abenza M, Reby D, & Mathevon N (2017). Dog-directed speech: why do we use it and do dogs pay attention to it? Proc R Soc B, 284(1846), 20162429. doi:10.1098/rspb.2016.2429

Author Manuscript Author Manuscript Author Manuscript Author Manuscript

Bensky MK, Gosling SD, & Sinn DL (2013). The world from a dog's point of view: a review and synthesis of dog cognition research Advances in the Study of Behavior (Vol. 45, pp. 209–406): Elsevier.

Bhattacharjee D, Dev N, Gupta S, Sau S, Sarkar R, Biswas A, … Bhadra A (2017). Free-ranging dogs show age related plasticity in their ability to follow human pointing. PloS one, 12(7). doi:10.1371/journal.pone.0180643

Bibost A-L, & Brown C (2014). Laterality influences cognitive performance in rainbowfish Melanotaenia duboulayi. Anim Cogn, 17(5), 1045–1051. doi:10.1007/s10071-014-0734-3 [PubMed: 24531906]

Branson N, & Rogers L (2006). Relationship between paw preference strength and noise phobia in Canis familiaris. J Comp Psychol, 120(3), 176–183. doi:10.1037/0735-7036.120.3.176 [PubMed: 16893254]

Bräuer J, Kaminski J, Riedel J, Call J, & Tomasello M (2006). Making inferences about the location of hidden food: social dog, causal ape. J Comp Psychol, 120(1), 38–47. doi:10.1037/0735-7036.120.1.38 [PubMed: 16551163]

Bray EE, Gruen M, Gnanadesikan GE, Horschler DJ, Levy K, Kennedy BS, … MacLean E (2020). Cognitive characteristics of 8- to 10-week-old assistance dog puppies. Anim Behav, 166C, 193–206. doi:10.1016/j.anbehav.2020.05.019

Bray EE, Levy KM, Kennedy BS, Duffy DL, Serpell JA, & MacLean EL (2019). Predictive models of assistance dog training outcomes using the Canine Behavioral Assessment and Research Questionnaire and a standardized temperament evaluation. Front Vet Sci, 6, 49. doi:10.3389/fvets.2019.00049 [PubMed: 30873418]

Bray EE, MacLean EL, & Hare B (2014). Context specificity of inhibitory control in dogs. Anim Cogn, 17(1), 15–31. doi:10.1007/s10071-013-0633-z [PubMed: 23584618]

Bray EE, Sammel MD, Cheney DL, Serpell JA, & Seyfarth RM (2017). The effects of maternal investment, temperament, and cognition on guide dog success. P Natl Acad Sci USA, 114(34), 9128–9133. doi:10.1073/pnas.1704303114

Bray EE, Sammel MD, Seyfarth RM, Serpell JA, & Cheney DL (2017). Temperament and problem solving in a population of adolescent guide dogs. Anim Cogn, 20(5), 923–939. doi:10.1007/s10071-017-1112-8 [PubMed: 28695349]

Brubaker L, Dasgupta S, Bhattacharjee D, Bhadra A, & Udell MA (2017). Differences in problem-solving between canid populations: Do domestication and lifetime experience affect persistence? Anim Cogn, 20(4), 717–723. doi:10.1007/s10071-017-1093-7 [PubMed: 28429096]

Brucks D, Marshall-Pescini S, Wallis LJ, Huber L, & Range F (2017). Measures of Dogs' Inhibitory Control Abilities Do Not Correlate across Tasks. Front Psychol, 8, 849. doi:10.3389/fpsyg.2017.00849 [PubMed: 28596749]

Burrows KE, Adams CL, & Spiers J (2008). Sentinels of safety: Service dogs ensure safety and enhance freedom and well-being for families with autistic children. Qual Health Res, 18(12), 1642–1649. doi:10.1177/1049732308327088 [PubMed: 18955467]

Caspi A, Roberts BW, & Shiner RL (2005). Personality development: Stability and change. Annu. Rev. Psychol., 56, 453–484. doi:10.1146/annurev.psych.55.090902.141913 [PubMed: 15709943]

Christie L-A, Studzinski CM, Araujo JA, Leung CS, Ikeda-Douglas CJ, Head E, … Milgram NW (2005). A comparison of egocentric and allocentric age-dependent spatial learning in the beagle dog. Prog Neuro-Psychopharmacol Biol Psychiatry, 29(3), 361–369.

Curb LA, Abramson CI, Grice JW, & Kennison SM (2013). The relationship between personality match and pet satisfaction among dog owners. Anthrozoös, 26(3), 395–404.

Doré FY, Fiset S, Goulet S, Dumas M-C, & Gagnon S (1996). Search behavior in cats and dogs: interspecific differences in working memory and spatial cognition. Anim Learn Behav, 24(2), 142–149.

Dorey NR, Udell MA, & Wynne CD (2010). When do domestic dogs, Canis familiaris, start to understand human pointing? The role of ontogeny in the development of interspecies communication. Anim Behav, 79(1), 37–41. doi:10.1016/j.anbehav.2009.09.032

Duffy D, Kruger K, & Serpell J (2014). Evaluation of a behavioral assessment tool for dogs relinquished to shelters. Preventive veterinary medicine, 117(3–4), 601. [PubMed: 25457136]

Author Manuscript Author Manuscript Author Manuscript Author Manuscript

Duranton C, & Gaunet F (2016). Effects of shelter housing on dogs' sensitivity to human social cues. J Vet Behav, 14, 20–27. doi:10.1016/j.jveb.2016.06.011

Fagnani J, Barrera G, Carballo F, & Bentosela M (2016). Is previous experience important for inhibitory control? A comparison between shelter and pet dogs in A-not-B and cylinder tasks. Anim Cogn, 19(6), 1165–1172. doi:10.1007/s10071-016-1024-z [PubMed: 27541147]

Fiset S, Beaulieu C, & Landry F (2003). Duration of dogs'(Canis familiaris) working memory in search for disappearing objects. Anim Cogn, 6(1), 1–10. doi:10.1007/s10071-002-0157-4 [PubMed: 12658530]

Flutre T (2020). Timothee flutre's personal r code in rutilstimflutre. https://github.com/timflutre/rutilstimflutre.

Fratkin JL, Sinn DL, Patall EA, & Gosling SD (2013). Personality consistency in dogs: a meta-analysis. PloS one, 8(1), e54907. doi:10.1371/journal.pone.0054907 [PubMed: 23372787]

Friedman J, Hastie T, & Tibshirani R (2009). Glmnet: Lasso and elastic-net regularized generalized linear models. R package version 4.0. https://cloud.r-project.org/package=glmnet.

Friedman J, Hastie T, & Tibshirani R (2010). Regularization paths for generalized linear models via coordinate descent. J Stat Softw, 33(1), 1–22. [PubMed: 20808728]

Gácsi M, Györi B, Virányi Z, Kubinyi E, Range F, Belényi B, & Miklósi Á (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. doi:10.1371/journal.pone.0006584 [PubMed: 19714197]

Gácsi M, Kara E, Belényi B, Topál J, & Miklósi Á (2009). The effect of development and individual differences in pointing comprehension of dogs. Anim Cogn, 12(3), 471–479. doi:10.1007/s10071-008-0208-6 [PubMed: 19130102]

Gergely A, Faragó T, Galambos Á, & Topál J (2017). Differential effects of speech situations on mothers' and fathers' infant-directed and dog-directed speech: An acoustic analysis. Sci Rep, 7(1), 1–10. doi:10.1038/s41598-017-13883-2 [PubMed: 28127051]

Goddard M, & Beilharz R (1984a). A factor analysis of fearfulness in potential guide dogs. Appl Anim Behav Sci, 12(3), 253–265. doi:10.1016/0168-1591(84)90118-7

Goddard M, & Beilharz R (1984b). The relationship of fearfulness to, and the effects of, sex, age and experience on exploration and activity in dogs. Appl Anim Behav Sci, 12(3), 267–278.

Goddard M, & Beilharz R (1986). Early prediction of adult behaviour in potential guide dogs. Appl Anim Behav Sci, 15(3), 247–260. doi:0.1016/0168-1591(86)90095-X

Güntürkün O, Ströckens F, & Ocklenburg S (2020). Brain Lateralization: A Comparative Perspective. Physiol Rev, 100(3), 1019–1063. doi:10.1152/physrev.00006.2019 [PubMed: 32233912]

Hall SS, MacMichael J, Turner A, & Mills DS (2017). A survey of the impact of owning a service dog on quality of life for individuals with physical and hearing disability: a pilot study. Health qual life out, 15, 59. doi:10.1186/s12955-017-0640-x

Hare B, Brown M, Williamson C, & Tomasello M (2002). The domestication of social cognition in dogs. Science, 298(5598), 1634–1636. doi:10.1126/science.1072702 [PubMed: 12446914]

Hare B, Call J, & Tomasello M (1998). Communication of food location between human and dog (*Canis familiaris*). Evol Commun, 2(1), 137–159. doi:10.1075/eoc.2.1.06har

Harvey ND, Craigon PJ, Blythe SA, England GC, & Asher L (2017). An evidence-based decision assistance model for predicting training outcome in juvenile guide dogs. PloS one, 12(6), e0174261. doi:10.1371/journal.pone.0174261 [PubMed: 28614347]

Harvey ND, Craigon PJ, Sommerville R, McMillan C, Green M, England GC, & Asher L (2016). Test-retest reliability and predictive validity of a juvenile guide dog behavior test. J Vet Behav, 11, 65–76. doi:10.1016/j.jveb.2015.09.005

Hastie T, Tibshirani R, Friedman J, & Franklin J (2005). The elements of statistical learning: Data mining, inference and prediction. Math Intell, 27(2), 83–85.

Hastie T, Tibshirani R, & Wainwright M (2015). Statistical learning with sparsity: the lasso and generalizations: CRC press.

Head E (2013). A canine model of human aging and Alzheimer's disease. Biochim Biophys Acta, 1832(9), 1384–1389. [PubMed: 23528711]

Author Manuscript Author Manuscript Author Manuscript Author Manuscript

Head E, Callahan H, Cummings B, Cotman C, Ruehl W, Muggenberg B, & Milgram N (1997). Open field activity and human interaction as a function of age and breed in dogs. Physiol Behav, 62(5), 963–971. [PubMed: 9333188]

Horn JL (1965). A rationale and test for the number of factors in factor analysis. Psychometrika, 30(2), 179–185. [PubMed: 14306381]

Hsu Y, & Serpell JA (2003). Development and validation of a questionnaire for measuring behavior and temperament traits in pet dogs. J Am Vet Med Assoc, 223(9), 1293–1300. [PubMed: 14621216]

Izquierdo A, & Jentsch JD (2012). Reversal learning as a measure of impulsive and compulsive behavior in addictions. Psychopharmacology, 219(2), 607–620. doi:10.1007/s00213-011-2579-7 [PubMed: 22134477]

Jones AC, & Gosling SD (2005). Temperament and personality in dogs (*Canis familiaris*): A review and evaluation of past research. Appl Anim Behav Sci, 95(1–2), 1–53. doi:10.1016/j.applanim.2005.04.008

Kaminski J, Schulz L, & Tomasello M (2012). How dogs know when communication is intended for them. Dev Sci, 15(2), 222–232. doi:10.1111/j.1467-7687.2011.01120.x [PubMed: 22356178]

Kruschke J (2014). Doing Bayesian data analysis: A tutorial with R, JAGS, and Stan: Academic Press.

LaFollette M, Rodriguez K, Ogata N, & O'Haire M (2019). Military Veterans and Their PTSD Service Dogs: Associations Between Training Methods, PTSD Severity, Dog Behavior, and the Human-Animal Bond. Front Vet Sci, 6(23), 1–11. doi:10.3389/fvets.2019.00023 [PubMed: 30723724]

Lampe M, Bräuer J, Kaminski J, & Virányi Z (2017). The effects of domestication and ontogeny on cognition in dogs and wolves. Sci Rep, 7, 11690. doi:10.1038/s41598-017-12055-6 [PubMed: 28916808]

Lazarowski L, & Dorman DC (2015). A comparison of pet and purpose-bred research dog (Canis familiaris) performance on human-guided object-choice tasks. Behav Process, 110, 60–67. doi:10.1016/j.beproc.2014.09.021

Lazarowski L, Krichbaum S, Waggoner LP, & Katz JS (2020). The development of problem- solving abilities in a population of candidate detection dogs (*Canis familiaris*). Anim Cogn. doi:10.1007/s10071-020-01387-y

Lazarowski L, Rogers B, Waggoner LP, & Katz JS (2019). When the nose knows: ontogenetic changes in detection dogs'(Canis familiaris) responsiveness to social and olfactory cues. Anim Behav, 153, 61–68. doi:10.1016/j.anbehav.2019.05.002

Lazarowski L, Strassberg LR, Waggoner LP, & Katz JS (2019). Persistence and human-directed behavior in detection dogs: Ontogenetic development and relationships to working dog success. Appl Anim Behav Sci, 220, 104860. doi:10.1016/j.applanim.2019.104860

Lazzaroni M, Marshall-Pescini S, Manzenreiter H, Gosch S, Přibilová L, Darc L, … Range F (2020). Why do dogs look back at the human in an impossible task? Looking back behaviour may be over-interpreted. Anim Cogn, 1–15. doi:10.1007/s10071-020-01345-8

MacLean EL, & Hare B (2018). Enhanced selection of assistance and explosive detection dogs using cognitive measures. Front Vet Sci, 5(236), 1–14. doi:10.3389/fvets.2018.00236 [PubMed: 29417054]

MacLean EL, Hare B, Nunn CL, Addessi E, Amici F, Anderson RC, … Zhao Y (2014). The evolution of self-control. Proc Natl Acad Sci USA, 111(20), E2140–E2148. doi:10.1073/pnas.1323533111 [PubMed: 24753565]

MacLean EL, Herrmann E, Suchindran S, & Hare B (2017). Individual differences in cooperative communicative skills are more similar between dogs and humans than chimpanzees. Anim Behav, 126, 41–51. doi:10.1016/j.anbehav.2017.01.005

Magat M, & Brown C (2009). Laterality enhances cognition in Australian parrots. Proc R Soc B, 276(1676), 4155–4162. doi:10.1098/rspb.2009.1397

Marshall-Pescini S, Virányi Z, Kubinyi E, & Range F (2017). Motivational Factors Underlying Problem Solving: Comparing Wolf and Dog Puppies' Explorative and Neophobic Behaviors at 5, 6, and 8 Weeks of Age. Front Psychol., 8(180). doi:10.3389/fpsyg.2017.00180

Author Manuscript Author Manuscript Author Manuscript Author Manuscript

Marshall-Pescini S, Virányi Z, & Range F (2015). The Effect of Domestication on Inhibitory Control: Wolves and Dogs Compared. PloS one, 10(2), e0118469. doi:10.1371/journal.pone.0118469 [PubMed: 25714840]

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. Curr Biol, 13(9), 763–766. doi:10.1016/S0960-9822(03)00263-X [PubMed: 12725735]

Miklósi Á, Polgárdi R, Topál J, & Csányi V (1998). Use of experimenter-given cues in dogs. Anim Cogn, 1(2), 113–121. doi:10.1007/s100710050016 [PubMed: 24399275]

Milgram NW, Head E, Muggenburg B, Holowachuk D, Murphey H, Estrada J, … Cotman C (2002). Landmark discrimination learning in the dog: effects of age, an antioxidant fortified food, and cognitive strategy. Neurosci Biobehav Rev, 26(6), 679–695. [PubMed: 12479842]

Milgram NW, Head E, Weiner E, & Thomas E (1994). Cognitive functions and aging in the dog: acquisition of nonspatial visual tasks. Behav Neurosci, 108(1), 57. [PubMed: 8192851]

Moffitt TE, Arseneault L, Belsky D, Dickson N, Hancox RJ, Harrington HL, … Ross S (2011). A gradient of childhood self-control predicts health, wealth, and public safety. Proc Natl Acad Sci USA, 108(7), 1–6.

O'Haire ME, & Rodriguez KE (2018). Preliminary efficacy of service dogs as a complementary treatment for posttraumatic stress disorder in military members and veterans. J Consult Clin Psychol, 86(2), 179. doi:10.1037/ccp0000267 [PubMed: 29369663]

Ollivier F, Plummer C, & Barrie K (2007). Ophthalmic examination and diagnostics. Part 1: the eye examination and diagnostic procedures. Veterinary ophthalmology. 4th ed. Ames, Iowa: Blackwell Publishing, 438–483.

Passalacqua C, Marshall-Pescini S, Barnard S, Lakatos G, Valsecchi P, & Previde EP (2011). Human-directed gazing behaviour in puppies and adult dogs, Canis lupus familiaris. Anim Behav, 82(5), 1043–1050. doi:10.1016/j.anbehav.2011.07.039

Piotti P, Szabó D, Bognár Z, Egerer A, Hulsbosch P, Carson RS, & Kubinyi E (2018). Effect of age on discrimination learning, reversal learning, and cognitive bias in family dogs. Learn Behav, 46(4), 537–553. doi:10.3758/s13420-018-0357-7 [PubMed: 30251103]

R Development Core Team. (2016). R: a language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from http://www.R-project.org

Reid HM, & Norvilitis JM (2000). Evidence for anomalous lateralization across domain in ADHD children as well as adults identified with the Wender Utah rating scale. J Psychiatr Res, 34(4–5), 311–316. doi:10.1016/S0022-3956(00)00027-3 [PubMed: 11104843]

Revelle W (2019). psych: Procedures for Psychological, Psychometric, and Personality Research. R package version 1.9.12. Retrieved from https://CRAN.R-project.org/package=psych

Rice WR, & Gaines SD (1994). 'Heads I win, tails you lose': testing directional alternative hypotheses in ecological and evolutionary research. Trends Ecol Evol, 9(6), 235–237. doi:10.1016/0169-5347(94)90258-5 [PubMed: 21236837]

Riedel J, Buttelmann D, Call J, & Tomasello M (2006). Domestic dogs (*Canis familiaris*) use a physical marker to locate hidden food. Anim Cogn, 9(1), 27–35. doi:10.1007/s10071-005-0256-0 [PubMed: 15846526]

Riedel J, Schumann K, Kaminski J, Call J, & Tomasello M (2008). The early ontogeny of human–dog communication. Anim Behav, 75(3), 1003–1014. doi:10.1016/j.anbehav.2007.08.010

Riemer S, Mills DS, & Wright H (2014). Impulsive for life? The nature of long-term impulsivity in domestic dogs. Anim Cogn, 17(3), 815–819. doi:10.1007/s10071-013-0701-4 [PubMed: 24136014]

Riemer S, Müller C, Virányi Z, Huber L, & Range F (2016). Individual and group level trajectories of behavioural development in Border collies. Appl Anim Behav Sci, 180, 78–86. doi:10.1016/j.applanim.2016.04.021 [PubMed: 28184101]

Rodriguez KE, Bryce CI, Granger DA, & O'Haire ME (2018). The effect of a service dog on salivary cortisol awakening response in a military population with posttraumatic stress disorder (PTSD). Psychoneuroendocrinology, 98, 202–210. doi:10.1016/j.psyneuen.2018.04.026 [PubMed: 29907299]

Author Manuscript Author Manuscript Author Manuscript Author Manuscript

Rodriguez KE, LaFollette MR, Hediger K, Ogata N, & O'Haire ME (2020). Defining the PTSD service dog intervention: perceived importance, usage, and symptom specificity of psychiatric service dogs for military veterans. Frontiers in psychology, 11, 1638. [PubMed: 32849004]

Rosati AG, Wobber V, Hughes K, & Santos LR (2014). Comparative developmental psychology: How is human cognitive development unique? Evol Psychol, 12(2), 448–473. doi:10.1177/147470491401200211 [PubMed: 25299889]

Rossano F, Nitzschner M, & Tomasello M (2014). Domestic dogs and puppies can use human voice direction referentially. Proc R Soc B, 281, 20133201. doi:10.1098/rspb.2013.3201

Schmidt SL, Carvaho ALN, & Simoes EN (2017). Effect of handedness on auditory attentional performance in ADHD students. Neuropsychiatr Dis Treat, 13, 2921. [PubMed: 29238197]

Scott JP, & Fuller JL (1965). Genetics and the Social Behavior of the Dog. Chicago: University of Chicago Press.

Sforzini E, Michelazzi M, Spada E, Ricci C, Carenzi C, Milani S, … Verga M (2009). Evaluation of young and adult dogs' reactivity. J Vet Behav, 4(1), 3–10. doi:10.1016/j.jveb.2008.09.035

Shaw GA, & Brown G (1991). Laterality, implicit memory and attention disorder. Educ Stud, 17(1), 15–23. doi:10.1080/0305569910170102

Simoes EN, Carvalho ALN, & Schmidt SL (2017). What does handedness reveal about ADHD? An analysis based on CPT performance. Res Dev Disabil, 65, 46–56. doi:10.1016/j.ridd.2017.04.009 [PubMed: 28433793]

Slabbert J, & Odendaal J (1999). Early prediction of adult police dog efficiency—a longitudinal study. Appl Anim Behav Sci, 64(4), 269–288. doi:10.1016/S0168-1591(99)00038-6

Stan Development Team. (2018). RStan: the R interface to Stan. R package version 2.17.3. http://mc-stan.org.

Starling MJ, Branson N, Thomson PC, & McGreevy PD (2013). Age, sex and reproductive status affect boldness in dogs. The Veterinary Journal, 197(3), 868–872. doi:10.1016/j.tvjl.2013.05.019 [PubMed: 23778256]

Svartberg K, Tapper I, Temrin H, Radesäter T, & Thorman S (2005). Consistency of personality traits in dogs. Anim Behav, 69(2), 283–291. doi:10.1016/j.anbehav.2004.04.011

Tapp PD, Siwak CT, Estrada J, Head E, Muggenburg BA, Cotman CW, & Milgram NW (2003). Size and reversal learning in the beagle dog as a measure of executive function and inhibitory control in aging. Learn Memory, 10(1), 64–73.

Tinbergen N (1963). On aims and methods of ethology. Zeitschrift für Tierpsychologie, 20(4), 410–433.

Tomkins LM, Thomson PC, & McGreevy PD (2010). First-stepping Test as a measure of motor laterality in dogs (*Canis familiaris*). J Vet Behav, 5(5), 247–255. doi:10.1016/j.jveb.2010.03.001

Tomkins LM, Thomson PC, & McGreevy PD (2012). Associations between motor, sensory and structural lateralisation and guide dog success. The Veterinary Journal, 192(3), 359–367. doi:10.1016/j.tvjl.2011.09.010 [PubMed: 22023850]

Tomkins LM, Williams K, Thomson P, & McGreevy P (2012). Lateralization in the domestic dog (Canis familiaris): Relationships between structural, motor, and sensory laterality. Journal of Veterinary Behavior, 7(2), 70–79.

Torchiano M (2020). effsize: Efficient Effect Size Computation. R package version 0.8.0. Retrieved from https://CRAN.R-project.org/package=effsize

Turcsán B, Tátrai K, Petró E, Topál J, Balogh L, Egyed B, & Kubinyi E (2020). Comparison of Behavior and Genetic Structure in Populations of Family and Kenneled Beagles. Front Vet Sci, 7(183). doi:10.3389/fvets.2020.00183

van Horik JO, Beardsworth CE, Laker PR, Whiteside MA, & Madden JR (2020). Response learning confounds assays of inhibitory control on detour tasks. Anim Cogn, 23(1), 215–225. doi:10.1007/s10071-019-01330-w [PubMed: 31758353]

van Horik JO, Langley EJ, Whiteside MA, Laker PR, Beardsworth CE, & Madden JR (2018). Do detour tasks provide accurate assays of inhibitory control? Proc R Soc B, 285(1875), 20180150. doi:10.1098/rspb.2018.0150

Author Manuscript Author Manuscript Author Manuscript Author Manuscript

Virányi Z, Gácsi M, Kubinyi E, Topál J, Belényi B, Ujfalussy D, & Miklósi Á (2008). Comprehension of human pointing gestures in young human-reared wolves (*Canis lupus*) and dogs (*Canis familiaris*). Anim Cogn, 11(3), 373–387. doi:10.1007/s10071-007-0127-y [PubMed: 18183437]

Wallis LJ, Range F, Müller CA, Serisier S, Huber L, & Virányi Z (2014). Lifespan development of attentiveness in domestic dogs: drawing parallels with humans. Front Psychol, 5, 71. doi:10.3389/fpsyg.2014.00071 [PubMed: 24570668]

Wallis LJ, Szabó D, & Kubinyi E (2020). Cross-Sectional Age Differences in Canine Personality Traits; Influence of Breed, Sex, Previous Trauma, and Dog Obedience Tasks. Frontiers in Veterinary Science, 6, 493. [PubMed: 31993445]

Watowich MM, MacLean EL, Hare B, Call J, Kaminski J, & Miklósi Á (2020). Age influences domestic dog cognitive performance independent of average breed lifespan. Anim Cogn. doi:10.1007/s10071-020-01385-0

Wells DL (2003). Lateralised behaviour in the domestic dog, Canis familiaris. Behavioural processes, 61(1–2), 27–35. [PubMed: 12543480]

Wells DL, Hepper PG, Milligan AD, & Barnard S (2017). Cognitive bias and paw preference in the domestic dog (*Canis familiaris*). J Comp Psychol, 131(4), 317–325. doi:10.1037/com0000080 [PubMed: 28517942]

Whiteside MA, Bess MM, Frasnelli E, Beardsworth CE, Langley EJ, van Horik JO, & Madden JR (2020). No evidence that footedness in pheasants influences cognitive performance in tasks assessing colour discrimination and spatial ability. Learn Behav, 48, 84–95. doi:10.3758/s13420-019-00402-8 [PubMed: 31916193]

Wilsson E, & Sundgren P-E (1997). The use of a behaviour test for the selection of dogs for service and breeding, I: Method of testing and evaluating test results in the adult dog, demands on different kinds of service dogs, sex and breed differences. Appl Anim Behav Sci, 53(4), 279–295. doi:10.1016/S0168-1591(96)01174-4

Wilsson E, & Sundgren P-E (1998). Behaviour test for eight-week old puppies—heritabilities of tested behaviour traits and its correspondence to later behaviour. Appl Anim Behav Sci, 58(1), 151–162. doi:10.1016/S0168-1591(97)00093-2

Wynne CD, Udell MA, & Lord KA (2008). Ontogeny's impacts on human-dog communication. Anim Behav, 76(4), e1–e4. doi:10.1016/j.anbehav.2008.03.010

Zaine I, Domeniconi C, & Wynne CD (2015). The ontogeny of human point following in dogs: When younger dogs outperform older. Behav Process, 119, 76–85. doi:10.1016/j.beproc.2015.07.004

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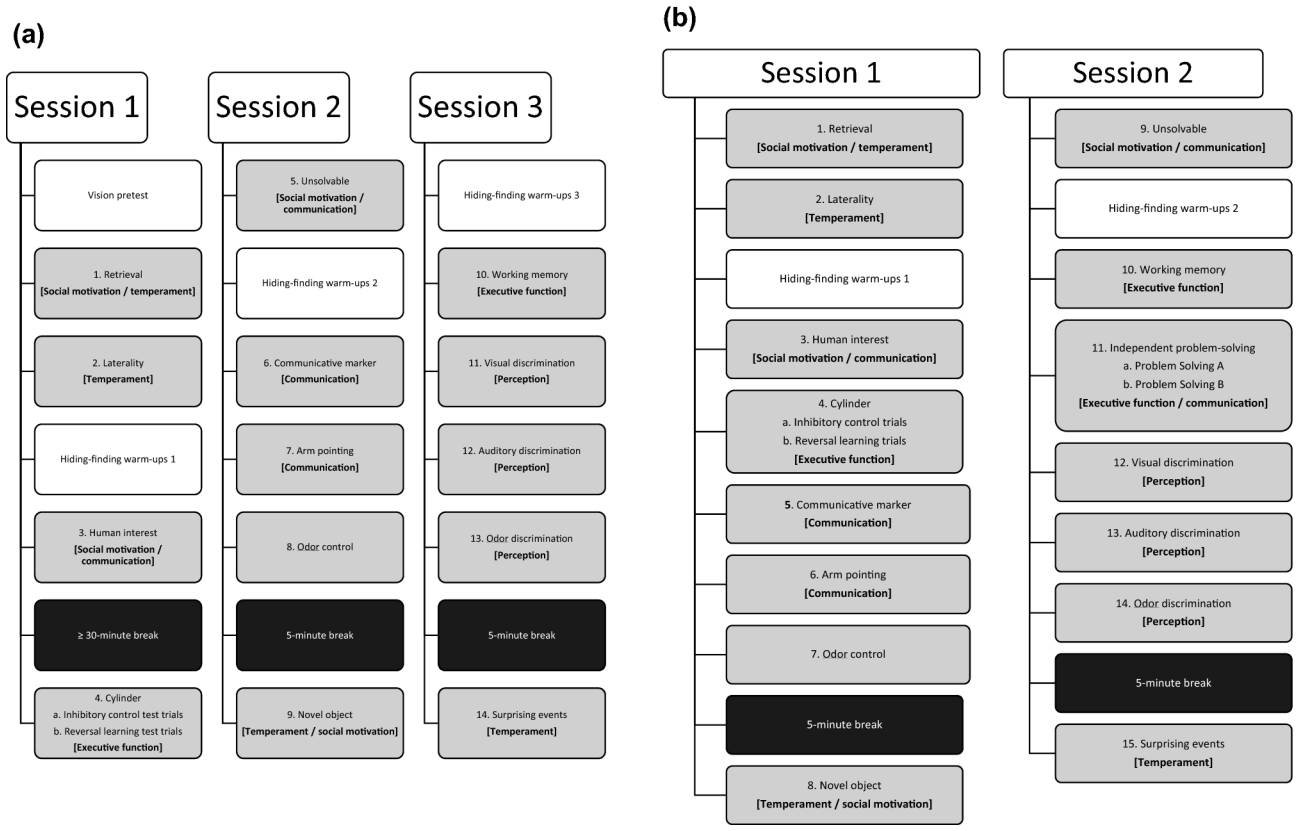

Fig 1.

Tasks comprising the Dog Cognitive Development Battery (DCDB). A) Order of DCDB tasks implemented in early development (~9 weeks), consisting of three ~45-minute sessions spread out over three days. B) Order of DCDB tasks implemented in early adulthood, consisting of two ~1–1.5-hour sessions administered either on the same day or over two consecutive days. In both panels, the constructs that each task was designed to measure are indicated in bold. A version of Fig. 1a was published in Animal Behaviour, 166, Bray EE, Gruen ME, Gnanadesikan GE, Horschler DJ, Levy KM, Kennedy BS, Hare BA, MacLean EL, Cognitive characteristics of 8- to 10-week-old assistance dog puppies, 193–206, Copyright (2020), reprinted with permission from Elsevier.

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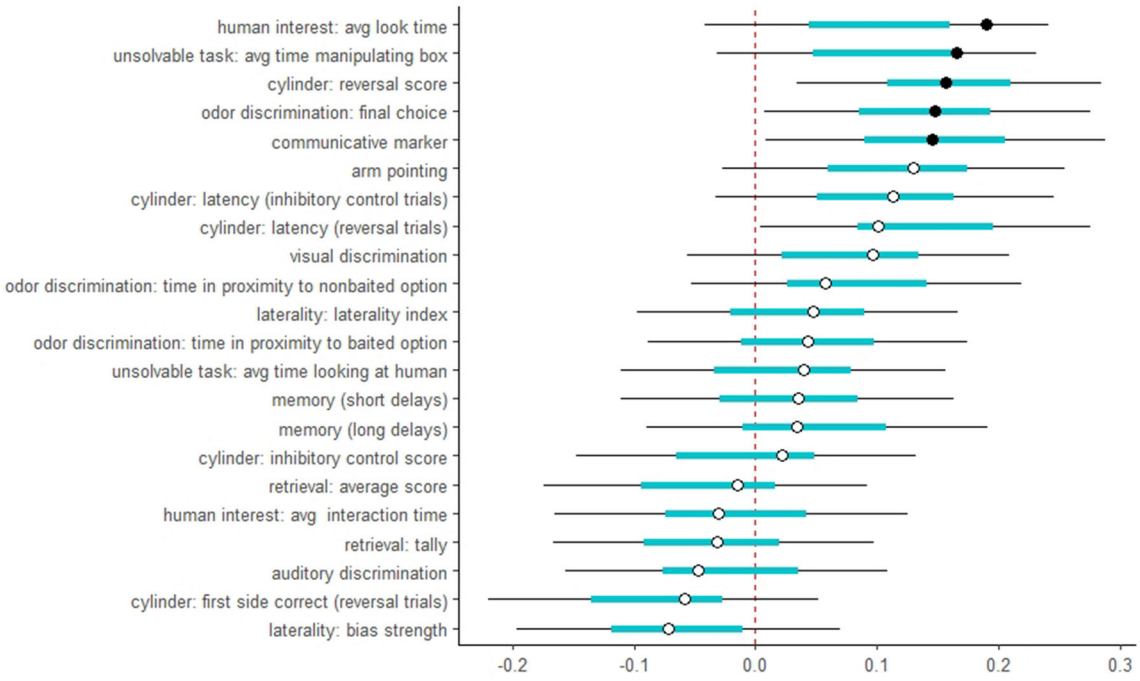

Fig 2.

Longitudinal stability of DCDB traits. Circles reflect the rank-order correlation coefficient between phenotypic measures collected from puppies and adults. Filled circles reflect significant correlations and open circles reflect correlations with p values > 0.05. For Bayesian mixed model analyses, the turquoise bars span the interquartile range of the posterior probability distribution for the beta coefficient relating puppy phenotypes and adult phenotypes; black lines span the 90% credible interval of the posterior distribution.

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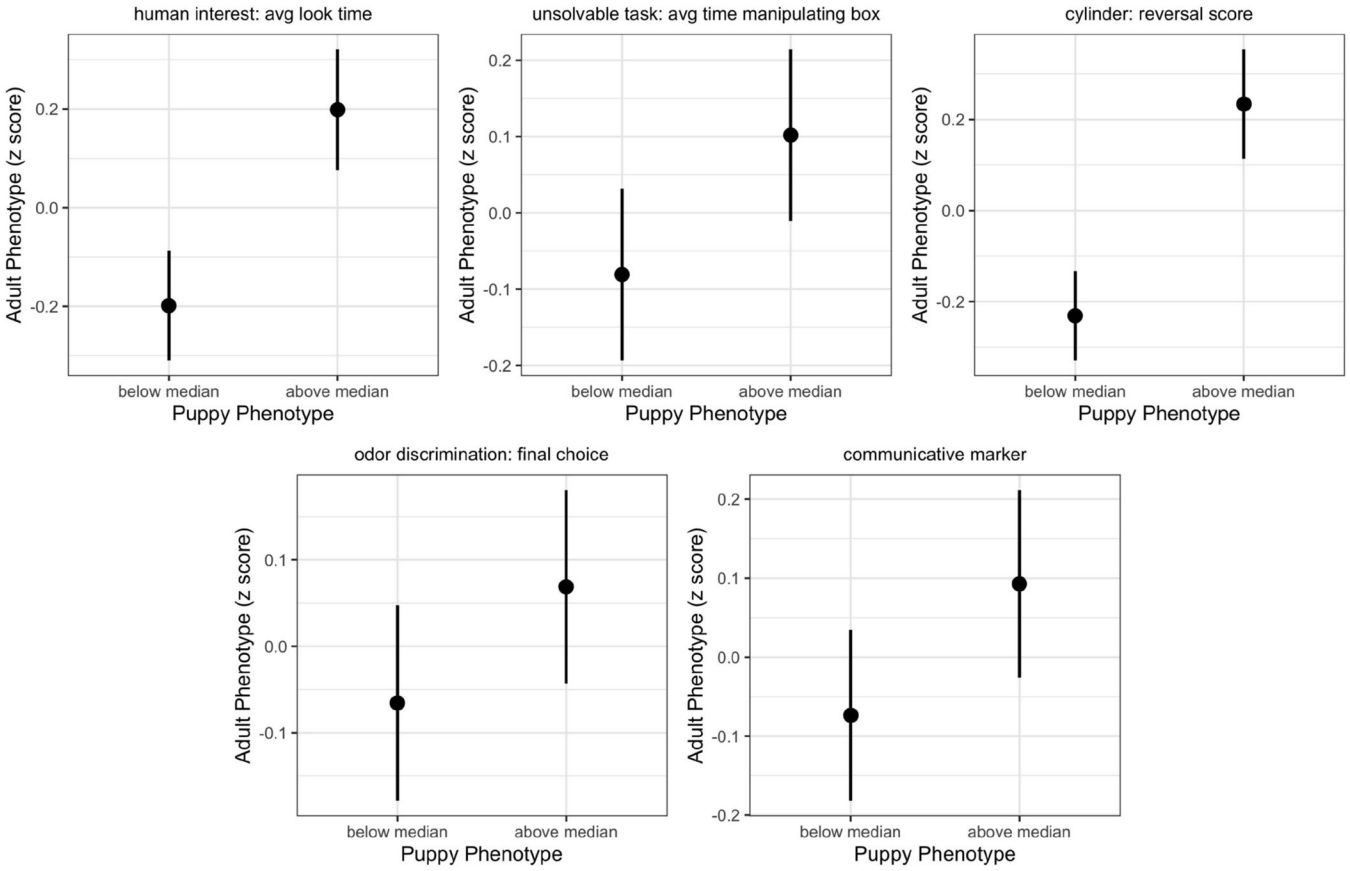

Fig 3.

Traits with significant longitudinal stability. Points and error bars reflect the mean and standard error of the adult phenotype

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Table 1.

Puppy DCDB predictor variables used in Lasso regressions.

task	measure	type of measure	variables into measure	proportion variance explained
Retrieval	Task engagement	Principal Component	average score (+), tally (+)	95%
Laterality	Laterality index	Z-scored variable	$\frac{[R-L]}{[R+L]} \times 100$	NA
Laterality	Bias strength	Z-scored variable	Absolute value of laterality index	NA
Human interest	Attentive	Principal Component	Average look time (+), average interaction time (+)	58%
Cylinder	Inhibitory control	Principal Component	Inhibitory control score (+)	24%
Cylinder	Reversal learning	Principal Component	Reversal score (+), first side correct (reversal trials) (+)	30%
Cylinder	Quick to solve	Principal Component	Latency (reversal trials) (−), latency (inhibitory control trials) (−)	30%
Unsolvable	Independent	Principal Component	Average time manipulating box (+), average time looking at human (−)	64%
Arm pointing	% trials correct	Z-scored variable	Arm pointing	NA
Communicative marker	% trials correct	Z-scored variable	Communicative marker	NA
Memory	% correct across delays	Principal Component	Short delays (+), long delays (+)	71%
Visual discrimination	% trials correct	Z-scored variable	Visual discrimination	NA
Auditory discrimination	% trials correct	Z-scored variable	Auditory discrimination	NA
Odor discrimination	Time spent near correct location	Principal Component	First choice (+), final choice (+), time in proximity to baited option (+), time in proximity to nonbaited option (−)	49%

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Table 2.

Adult DCDB outcome measures used in Lasso regressions.

task	measure	type of measure	variables into measure	proportion variance explained
Retrieval	Task engagement	Principal Component	Average score (+), tally (+)	95%
Laterality	Laterality index	Z-scored variable	$\frac{[R-L]}{[R+L]} \times 100$	NA
Laterality	Bias strength	Z-scored variable	Absolute value of laterality index	NA
Human interest	Average look time	Z-scored variable	Average look time	NA
Human interest	Average interaction time	Z-scored variable	Average interaction time	NA
Cylinder	Inhibitory control	Principal Component	Inhibitory control score (+), latency (inhibitory control trials) (−)	28%
Cylinder	Reversal learning	Principal Component	Reversal score (+), latency (reversal trials) (−), first side correct (reversal trials) (+)	38%
Unsolvable	Independent	Principal Component	Average time manipulating box (+), average time looking at human (−)	82%
Arm pointing	% trials correct	Z-scored variable	Arm pointing	NA
Communicative marker	% trials correct	Z-scored variable	Communicative marker	NA
Memory	% correct across delays	Principal Component	Short delays (+), long delays (+)	62%
Visual discrimination	% trials correct	Z-scored variable	Visual discrimination	NA
Auditory discrimination	% trials correct	Z-scored variable	Auditory discrimination	NA
Odor discrimination	Time spent near correct location	Principal Component	First choice (+), final choice (+), time in proximity to baited option (+), time in proximity to nonbaited option (−)	62%
Problem solving A	Success	Principal Component	Correct attempts (+), incorrect attempts (+), latency to solve (−), gaze (−), engage (+)	68%

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Table 3.

Summary of primary analyses.

Statistical Method	Question assessed	Results
Paired-sample t-tests	mean changes across development	Table 4
Spearman correlations	rank-order stability of individual differences	Figure 2
Bayesian linear mixed models	longitudinal trait stability controlling for covariates and genetic relatedness	Figure 2
Lasso regression	associations between puppy phenotypes and adult phenotypes (multiple regression with variable selection)	Table 5

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Table 4.

Within-subject age differences by task. Medium to large effect sizes are indicated in bold.

variable	units	puppy mean	adult mean	t	df	p	effect size (Cohen's d)	lower 95% CI	upper 95% CI
retrieval: average score	rating system (see text)	3.3	3.7	2.96	159	< 0.01	0.23	0.08	0.39
retrieval: tally	No. tallies	3.01	6.17	5.46	159	< 0.01	0.43	0.27	0.59
laterality: laterality index	$\frac{[R-L]}{[R+L]} \times 100$	−7.71	−10.7	−0.48	159	0.63	−0.04	−0.19	0.12
laterality: bias strength	absolute value of laterality index	40.88	59.06	5.40	159	< 0.01	0.43	0.26	0.59
human interest: avg look time	No. of seconds	6.44	15.55	13.62	141	< 0.01	**1.14**	0.93	1.35
human interest: avg interaction time	No. of seconds	18.57	19.32	1.20	141	0.23	0.10	−0.06	0.27
cylinder: inhibitory control score	% trials correct	51.19	75.94	9.75	157	< 0.01	**0.78**	0.60	0.95
cylinder: latency (inhibitory control trials)	No. of seconds	3.99	3.35	−2.54	157	0.01	−0.20	−0.36	−0.04
cylinder: reversal score	% trials correct	29.7	59.59	11.53	155	< 0.01	**0.92**	0.73	1.11
cylinder: first side correct (reversal trials)	% trials correct	23.01	57	9.99	155	< 0.01	**0.80**	0.62	0.98
cylinder: latency (reversal trials)	No. of seconds	6.65	6.25	−0.96	155	0.34	−0.08	−0.23	0.08
unsolvable task: avg time looking at human	No. of seconds	0.98	3.3	7.79	158	< 0.01	**0.62**	0.45	0.79
unsolvable task: avg time manipulating box	No. of seconds	12.78	13.51	1.40	158	0.16	0.11	−0.05	0.27
arm pointing	% trials correct	69.5	77.14	3.75	155	< 0.01	0.30	0.14	0.46
communicative marker	% trials correct	76.11	89.32	8.25	157	< 0.01	**0.66**	0.48	0.83
memory (short delays)	% trials correct	63.22	73.09	2.41	57	0.02	0.32	0.05	0.58
visual discrimination	% trials correct	91.33	90.08	−0.90	159	0.37	−0.07	−0.23	0.08
auditory discrimination	% trials correct	59.2	65.47	2.87	158	< 0.01	0.23	0.07	0.39
odor discrimination: first choice	% trials correct	53.31	60.94	3.35	155	< 0.01	0.27	0.11	0.43
odor discrimination: final choice	% trials correct	72.22	71.77	−0.25	155	0.81	−0.02	−0.18	0.14
odor discrimination: time in proximity to baited option	No. of seconds	61.32	64.33	1.14	155	0.26	0.09	−0.07	0.25
odor discrimination: time in proximity to non-baited option	No. of seconds	18.35	20.7	1.92	155	0.06	0.15	−0.00	0.31

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Table 5.

Linear models predicting adult phenotypes from puppy phenotypes. Significant predictors are indicated in bold.

adult outcome	puppy predictor	β	t	p
human interest: avg look time $r^2 = 0.17$	communicative marker	0.0906	1.1517	0.2512
	arm pointing	**0.2216**	**2.8286**	**0.0053**
	retrieval (high engagement)	**0.2027**	**2.6959**	**0.0078**
	memory: all delays	**0.1511**	**2.0418**	**0.0429**
auditory discrimination $r^2 = 0.11$	arm pointing	0.1268	1.6908	0.0929
	visual discrimination	0.1401	1.5459	0.1242
	human interest: attentive	0.1241	1.7182	0.0878
	cylinder: reversal learning	**0.2446**	**3.4026**	**0.0000**
	memory: all delays	−0.0496	−0.686	0.4937
problem solving A: success $r^2 = 0.30$	laterality: laterality index	0.1208	1.7173	0.088
	visual discrimination	−0.1064	−1.2165	0.2257
	auditory discrimination	**0.1431**	**1.9663**	**0.0511**
	retrieval (high engagement)	**0.2485**	**3.5372**	**0.0000**
	cylinder: reversal learning	−0.0656	−0.9478	0.3448
cylinder: reversal learning $r^2 = 0.11$	**cylinder: quick to solve**	**0.1557**	**2.0561**	**0.0414**
	cylinder: inhibitory control	**0.1759**	**2.3023**	**0.0226**
	unsolvable: independent	0.12	1.5727	0.1178
cylinder: inhibitory control $r^2 = 0.07$	**laterality: laterality index**	**0.1842**	**2.3505**	**0.0200**
	memory: all delays	**0.1809**	**2.346**	**0.0202**
memory: all delays $r^2 = 0.04$	laterality: bias strength	0.1435	1.7640	0.0797
	communicative marker	0.1239	1.4890	0.1385