

Cognitive development of detection dogs

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Abstract

The question of the extent to which cognitive capabilities predict future outcomes has been long pursued across several species. Also of interest are the evolutionary implications of the comparative study of cognitive abilities. The cognitive skills of dogs have been extensively assessed, but have been limited to domesticated and encultured populations such as pet dogs. The resulting literature overlooks other important populations and also has largely neglected to investigate developmental effects, which are critical to understanding the evolutionary and ontogenetic origins of canine cognition. In this dissertation, I explore the cognitive development and its relationship to future outcomes in a group of candidate detector dogs. Chapters 2 and 3 evaluate the performance of dogs on two commonly used tasks of canine social cognition, expanding to assess the application of such measures to detection dog performance and selection. Chapter 2 investigates alternative uses of the ‘Unsolvable Task’ for quantifying traditionally subjective measures of working dog behavioral characteristics, as well as evaluating the developmental trajectory of behaviors measured in the task. Chapter 3 examines detection dogs’ bias when presented with conflicting social and olfactory cues using the object-choice task. Chapters 4 and 5 explore non-social cognition in detection dogs, assessing inhibitory control (Chapter 4) and physical problem-solving (Chapter 5). Taken together, dogs showed developmental increases in social cognition and problem-solving skills, with variation in performance predictive of detection dog outcomes. These findings provide insights into the

developmental and phylogenetic origins of canine cognition, extending findings to a new population of canines with important practical implications.

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Table of Contents

Abstract.....	ii
Acknowledgments.....	iv
List of Tables	viii
List of Figures	ix
Chapter 1: General Introduction	1
Introduction	1
Dissertation Outline	5
References	6
Chapter 2: Persistence and gaze alternation in detection dogs: ontogenetic development and relationships to success.....	10
Introduction	10
Methods	16
Results	21
Discussion	24
References	30
Chapter 3: Ontogenetic effects on responsiveness to social and olfactory cues in detection dogs.....	37
Introduction	37
Methods	42
Results	46

Discussion	47
References	50
Chapter 4: Development of inhibitory control in relation to detection dog success.....	60
Introduction	60
Methods	68
Results	73
Discussion	78
References	84
Chapter 5: Ontogeny of detection dogs' understanding of hidden objects.....	95
Introduction	95
Methods	102
Results	106
Discussion	109
References	119
Chapter 6: Conclusions.....	129
Appendix.....	132

List of Tables

Table 2-1	34
-----------------	----

List of Figures

Figure 2-1	35
Figure 2-2	36
Figure 3-1	57
Figure 3-2.....	58
Figure 3-3.....	59
Figure 4-1.....	92
Figure 4-2.....	93
Figure 4-3.....	94
Figure 5-1.....	124
Figure 5-2.....	125
Figure 5-3.....	126
Figure 5-4.....	127
Figure 5-5.....	128

Chapter I: General Introduction

The study of canine cognition is a recently emerging but thriving field, likely owing to the significant roles dogs play in human society both as companion animals assimilated into the social network of the human family, as well as in various occupational roles benefiting human welfare (Helton, 2009; Miklósi, 2015). The unique niche filled by dogs likely results from selection pressures during domestication, in which a symbiotic mutualism experienced between dogs and humans may have driven a selection for dogs' ability to communicate and cooperate with people (Kaminski & Marshall-Pescini, 2014). These selection pressures are thought to have given rise to sophisticated social skills for interacting with people similar to those appearing early in human development, unrivaled by other species including nonhuman primates (MacLean, Herrmann, Suchindran, & Hare, 2017). Based on these findings, the Domestication Hypothesis posits that selection for sensitivity to human social cues that occurred during domestication led to an innate enhanced understanding of and responsiveness to human behavior, further supported by evidence that dogs outperform wolves, their own closest ancestor. Conversely, the Two-Stage hypothesis proposes that these abilities are not innate and require 1) socialization to humans during the critical developmental window and 2) learning and experience with relevant human gestures, and is supported by evidence that experience can greatly modulate these abilities (Udell, Dorey, & Wynne, 2010). Though the debate continues, it is evident that both phylogeny and ontogeny are important for the development of dogs' ability to utilize social information from humans (Udell & Wynne, 2010). On the other hand, apes outperform dogs on cognitive tasks involving physical (e.g., non-social) cognition (Bräuer, Kaminski, Riedel, Call, & Tomasello, 2006; Rooijackers, Kaminski, & Call, 2009), leading to the hypothesis that while domestication may have selected for sophisticated socio-cognitive abilities in dogs, it also

alleviated selection pressures in the physical domain because dogs were becoming less independent and more reliant on humans. However, it is again possible that experience rather than domestication may be responsible for these differences in physical cognition between dogs and other species. Dogs living in human homes typically do not face challenges requiring physical problem-solving skills, and thus have limited opportunities to gain experience in the physical domain (Müller, Riemer, Virányi, Huber, & Range, 2016). Relative to investigations of canine social cognition, much less is known about abilities pertaining to physical domains.

A notable limitation in the canine cognition literature is that much of the research has been restricted to testing populations of pet dogs. Pet dogs living in human homes have unique life histories and experiences that make it difficult to disentangle the relative contributions of domestication and experience, and make comparisons to non-domesticated species problematic. Thus, broad conclusions about the origins of canine cognition based on these potentially biased samples should be interpreted cautiously. Recently, efforts have been made to diversify the literature and address these questions by including other populations of both domesticated and wild canids such as socialized wolves and feral dogs. One population that has been largely overlooked is that of working dogs, which have been bred and trained to perform specific tasks, and therefore represent a group of domesticated dogs with vastly contrasting experiences compared to pet dogs. The unique experiences in regard to rearing, human interaction, and training undergone by working dogs may have led to a unique set of social and physical problem-solving skills. Thus, such populations may offer valuable insights into the extents and limitations of canine cognition.

Humans have benefited from a working relationship with dogs for centuries dating back to ancient times, using dogs for hunting, guarding, herding, and war (Miklósi, 2015). Working

dogs, defined as any domestic dog that is operational in private industry, government, assistance, or sporting contexts (Cobb, Branson, McGreevy, Lill, & Bennett, 2014), currently serve a diverse range of functions in modern society including police work, assistance to the blind or physically disabled, therapy and emotional support, search and rescue, and detection of a wide variety of substances (Miklósi, 2015). For example, dogs have been trained to detect explosives (Furton & Myers, 2001), narcotics (Minhinnick et al., 2017), cancers (Willis et al., 2004), live viruses (Angle et al., 2016), pests (Cooper, Wang, & Singh, 2014), and wildlife (Beebe, Howell, & Bennett, 2016). The emergence of more modern functions of working dogs has influenced the specific skills required of the dogs as well as the relationship between dogs and humans in these roles (Miklósi, 2015).

Dogs trained for explosives detection are widely considered the most efficient and effective technology available (Helton, 2009). However, the working dog industry faces challenges stemming from the laborious and costly nature of breeding, selecting, training, and housing dogs, with the added uncertainty of success (Beebe et al., 2016). It has been estimated that approximately 50% of dogs trained for working roles fail to become operational (Cobb et al., 2014). Not surprisingly, a great deal of emphasis in the working dog industry is placed on the selection of dogs suitable for specific working roles. Various factors may contribute to the attrition that occurs from the point of selection to eventual placement into an occupational role, and researchers have identified a clear need for the development of standardized tools that may improve the selection process (Beebe et al., 2016).

The majority of research on selection has focused on temperament, defined as consistent individual differences in behavioral phenotypes (Graham & Gosling, 2009; Sinn, Gosling, & Hilliard, 2010). Commonly assessed categories of temperamental traits in working dogs include

fearfulness, trainability, sociability (e.g., cooperation with handler), and aggression (Beebe et al., 2016; Maejima et al., 2007). However, temperament tests tend to be problematic in predicting working dog suitability because many traits are subjective and difficult to quantify, can be context-specific, and exhibit a large degree of variability in their validity (Miklósi et al., 2014). Emphasis has also been placed on the importance of selecting based on motivational drives (e.g., object obsession, play, and hunt drives), but these terms also lack standardization and are therefore difficult to measure. Perhaps the greatest quest in working dog selection has been to develop tests that predict a young puppy's future behavior, which has obvious implications for selecting potentially suitable dogs for specific training programs and eliminating unsuccessful dogs before investing unnecessary time and resources (Miklósi, 2015; Riemer, Müller, Virányi, Huber, & Range, 2014). However, research on the validity of puppy tests as well as precisely at which age future behavior can be reliably predicted has yielded mixed results (Slabbert & Odendaal, 1999; Svobodová, Vápeník, Pinc, & Bartoš, 2008; Wilsson & Sundgren, 1998), and the utility of puppy tests for consistently predicting future behavior has been questioned (Miklósi, 2015). Taken together, there remains a need for developing operational definitions of the traits predictive of working dog success (Beebe et al., 2016).

Cognitive abilities are likely a critical factor in successful working dog performance, but investigations of cognitive abilities unique to working dogs and their potential applications to selection and training are limited. Detection work, for example, requires learning numerous conditional discriminations and appropriate responses, memory for various targets, and skills enabling spatial navigation. Additionally, training requires aspects of social cognition including responsiveness to commands and cooperation with handlers, and thus involves various underlying cognitive processes (Lit, 2009). Therefore, there is potential merit in identifying the

cognitive processes important to working dog success; understanding the cognitive mechanisms related to working dog behaviors that are critical for success may help operationalize subjective terms often used in the field, improving the selection process.

Due to gaps in the canine cognition literature, and the need for improving identification of the characteristics predictive of working dog success, applying commonly-used measures of cognition to populations of working dogs has several promising implications. For one, assessing the cognitive abilities of a population of domestic dog with contrasting life history and experience to pet dogs may shed light into the phylogenetic and ontogenetic development of social and physical cognition. Second, given the limitations of current methods used to identify successful working dog characteristics, exploring the role of cognition may result in valuable methods for characterizing these critical skills.

Dissertation outline

This dissertation sought to characterize the development of a diverse range of cognitive abilities in candidate detection dogs, and determine their value in predicting detection dog suitability. A subset of tests derived from the 25-item Dog Cognition Test Battery (DCTB) (MacLean et al., 2017) were selected based on their potential relevance to detection dogs, with three tasks each pertaining to social, physical, and general cognitive domains. Chapters 2 and 3 of the dissertation evaluate the performance of detection dogs on two commonly used tasks of canine social cognition. Chapter 2 investigates alternative uses of the ‘Unsolvable Task’ for quantifying traditionally subjective measures of working dog behavioral characteristics, as well as evaluating the developmental trajectory of behaviors measured in the task. Chapter 3 examines detection dogs’ cue preference when presented with conflicting social and olfactory information using the object-choice task, which has been used exhaustively with pet dogs but has

rarely been utilized in working populations. Chapters 4 and 5 examine non-social cognition in detection dogs; Chapter 4 specifically focuses on inhibitory control, an emerging topic of study in canine cognition that has not been adequately explored in working populations. Chapter 5 focuses on aspects of working memory and object permanence in detection dogs' search for hidden objects using three different tasks.

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Chapter II. Persistence and human-directed behavior in detection dogs: ontogenetic development and relationships to working dog success

Due to their unrivaled olfactory abilities, dogs are being increasingly utilized for specialized scent detection tasks. However, current methods for identifying successful candidates are inadequate and not able to keep up with growing demands. Given that behavioral factors are the greatest predictor of working dog success or failure, developing better methods for their identification is critical. In the current study, we applied a common canine problem-solving measure to a population of candidate detection dogs. Dogs were tested on the unsolvable task, which assessed both human- and task-oriented behaviors, in three cross-sectional groups across their first year. We found that both human-oriented gazing and task persistence increased with age, and aspects of test performance were predictive of future detector dog success. These findings contribute to the investigation of the origins of dogs' cognitive abilities providing insights into ontogenetic factors, and have important implications for working dog selection and training.

1. Introduction

The unrivaled olfactory abilities of dogs have led to the increasing use of scent detection dogs for combating emerging societal and ecological threats such as person-borne moving explosives (Lazarowski et al., 2018), cancers (Edwards et al., 2017), and endangered and invasive species (Beebe et al., 2016). Escalations in terrorism and corresponding elevated security requirements have driven a particular rise in the demand for dogs trained to detect explosives (Hayes et al., 2018), and recent reports have warned of shortages in the breeding stock supply necessary to meet these demands (Murphy, 2017). Further, the working dog

industry continuously struggles with candidate attrition, which is exacerbated by a lack of standardized and objective tools that would allow for the early identification of dogs suitable for service (Jamieson et al., 2017).

Behavioral characteristics are critical to a working dogs' success and are given the utmost consideration in the selection of potential candidates. In particular, a dog's inherent motivational drives are universally acknowledged as essential traits for successful detection dogs (Beebe et al., 2016). Several different types of drives have been described in the literature as important for detection dogs including play, food, and prey drives, with simply 'drive' often used as a blanket term referring to a dog's general motivation to work. Because training detection dogs relies heavily on reward-based methods using combinations of toy, food, and social reinforcement, strong motivational drives allow for more efficient training as well as maintaining consistent search endurance over long periods of time and strenuous environmental conditions (Brownell & Marsolais, 2002). Despite the pervasive acknowledgement of the importance of drive and drive testing, it is widely regarded as a rather ambiguous quality that is difficult to operationalize and quantify, and therefore problematic as a selection measure. Thus, interpretations, definitions, and relative value of drive as a selection tool vary significantly among scientific and training communities.

A promising tool for measuring a dog's working potential is the 'Unsolvable Task', originally developed as a test of social cognition in companion dogs, which presents a desirable but inaccessible reward to dogs (i.e., a treat or toy inside a locked transparent container) and measures dogs' subsequent behavior (Miklósi et al., 2000). The task has traditionally been used to measure dogs' tendency to look to a human for help, which has been interpreted as a communicative mechanism indicative of joint attention (Marshall-Pescini et al., 2009). For

example, dogs have been shown to demonstrate gaze alternation when faced with the unsolvable task, rapidly alternating eye gaze between the desired object and a bystander as if attempting to direct the person's attention to the object. Gaze alternation is considered a more sophisticated form of active information transfer and is well-established in typically-developing children (Miklósi et al., 2000). Decreases in gaze alternation when either the reward or the human is absent or inattentive further implies gaze-alternation as a social behavior with communicative intent (Marshall-Pescini, et al., 2013; Miklósi et al., 2000). Hence, dogs' tendency to look to humans for help has been considered evidence of dogs' unique communicative abilities with humans.

On the other hand, alternative behaviors to gazing at humans during the unsolvable task may also be informative. For example, persisting in attempting to solve the task may be an indication of independence and motivation. Thus, dogs with greater motivational drives may persist longer on the unsolvable task in an attempt to obtain the inaccessible reward, and more independent dogs may be less likely to solicit help from humans. Persistence is a desirable trait in detection dogs due to the presence of environmental distractions and the low probability of encountering a target, and thus subsequent reinforcement, in operational contexts (Hall, 2017). Persistence during the unsolvable task has been suggested as a measure of resistance to extinction (Hall, 2017), and given the similarities to definitions of drive, may be a more useful and objective metric for characterizing the concept of drive in working dogs.

Both phylogenetic and ontogenetic factors have been shown to influence human-directed behaviors and persistence in problem-solving tasks in varying populations of canids. For example, studies showing heritability of human-directed attention-seeking (Persson et al., 2015) and associations between human-directed gazing and polymorphisms in the dopamine receptor

D4 gene in the unsolvable task indicate a genetic basis of such behaviors (Hori et al., 2013). Further, studies have shown that human-socialized wolves gaze less at humans and persist longer during problem-solving tasks compared to dogs, including free-ranging dogs with presumably minimal human experience (Marshall-Pescini et al., 2017; Miklosi et al., 2003; Udell, 2015). These dog-wolf differences suggest that domestication may have selected for a tendency to rely on humans to solve problems, thereby reducing independent problem-solving. Reported breed differences in gazing also suggest genetic influences. For example, dogs from hunting and herding breeds which have been selectively bred for working in concert with people (e.g., border collies and golden retrievers) have been shown to gaze at humans during the unsolvable task more than dogs from breeds that did not experience selection for such traits (Konno et al., 2016; Passalacqua et al., 2011).

While these findings suggest that domestication and selective breeding enhanced human-directed gazing, the role of experience cannot be ruled out. For example, dogs from cooperative working breeds are more likely to be used in breed-related interactive activities with their owners resulting in differential experiences (Udell et al., 2014), which is supported by the finding that breed differences in unsolvable task performance become more pronounced with age (Passalacqua et al., 2011). In fact, other studies have shown that training and rearing history influences human-directed behavior during the unsolvable task. For example, dogs trained in tasks that require cooperation with a handler such as agility, search and rescue, and water rescue gazed longer at humans or alternated gaze more frequently than untrained pets (D'Aniello et al., 2015; Marshall-Pescini et al., 2009). Conversely, trained guide dogs gazed at humans less than untrained dogs, which may be a product of the independence fostered in guide dog training (D'Aniello & Scandurra, 2016; Scandurra et al., 2015). Similarly, dogs with more training spent

more time interacting with the apparatus in an attempt to independently solve the task (Marshall-Pescini et al., 2016), and guide dogs that had been living in a human home for one year gazed at humans more than dogs near completion of training and still residing in a kennel. Dogs residing in a kennel since birth also gazed at humans less than dogs kept as pets (D'Aniello & Scandurra, 2016). Effects of experience are also supported by reports of human-directed gazing during the unsolvable task increasing with age (Konno et al., 2016; Passalacqua et al., 2011b; Persson et al., 2015). Taken together, it appears that while there may be an evolutionary basis to dogs' readiness to attend to humans and inhibit independent problem-solving, experience can greatly modulate these effects.

Though the effects of training and experience on dogs' use of human-directed behaviors have been thoroughly examined, how such behaviors may relate to working dog success has not. Additionally, non-social uses of the unsolvable task (i.e., persistence and independence) are sparse, especially in working dog contexts. Given that type and level of training has been shown to influence behaviors on the unsolvable task, we may expect to see a relationship between the development of such behaviors and working dog success. On one hand, training involving cooperation and synchronization with humans has been shown to increase human-directed behaviors, as these behaviors are encouraged in training requiring close contact with people. Dogs that are more attentive and sensitive to humans may also be likely to be more successful in roles requiring cooperation with humans. On the other hand, roles requiring dogs to work independently and not be influenced by potential human biasing (e.g., detection dogs) may show less human-directed behaviors and greater persistence as a result of training. Likewise, dogs showing a greater tendency to rely on humans in the unsolvable task may generally be overly dependent on humans, an undesirable trait in some types of working dogs. Brubaker et al. (2018)

recently tested a similar hypothesis by comparing search and rescue dogs to pet dogs in a puzzle box problem-solving task. The authors' predictions that search and rescue dogs would outperform pets in their persistence and problem-solving success due to training to work independently was not supported; however, search and rescue dogs typically live in homes with their owner/handler and thus are essentially comparable to pets in many aspects that may influence problem-solving behavior and override effects of training. Further, as noted by the authors, search and rescue dogs must maintain some degree of visual contact with their handlers during search, and must be vigilant of both handler signals and cues as well as other human cues that may lead to the discovery of a victim. Exploring persistence and human-directed behaviors in relation to performance in working dogs that must truly work autonomously and explicitly ignore human interference, such as detection dogs, may be useful in developing more objective definitions of important working dog characteristics, and may lead to improvements in training and selection.

The objective of the current study was to determine ontogenetic effects (i.e., age and experience) on unsolvable task performance in detection dogs, and to assess the potential applicability of the unsolvable task to detection dog selection. Few studies have assessed developmental changes in unsolvable task performance, and examinations of such effects in working dog populations are especially lacking. Given ongoing questions regarding the relative roles of genetic factors (e.g., domestication, breed, etc.) and lifetime experiences (e.g., experience with humans, formal training, etc.) on dogs' socio-cognitive and problem-solving abilities, applying the unsolvable task to working dog populations with distinct and controlled genetic and lifetime experiences may provide further insights into the origins of canine cognition. We hypothesized that a population of purpose-bred detection dogs residing in a kennel

environment would show reduced human-directed behaviors (e.g., gaze alternation) during the unsolvable task and later emergence of such behaviors due to differences in environmental histories with respect to opportunities to learn about human communication compared to pet dogs. Similarly, we predicted that detection dogs would show greater levels of independence and persistence due to less experience relying on humans as well as explicit training in working independently. With respect to the utility of the unsolvable task in identifying successful versus unsuccessful candidate detection dogs, we anticipated that dogs showing greater independence and persistence with less dependence on humans would be more successful detection dog candidates. By using a developmental approach, any early predictors of future success may be identified. The use of a homogenous sample with controlled genetic and environmental histories eliminates confounds of breed differences or variations in housing, enrichment, or past experiences that could contribute to cognitive differences (Arden & Adams, 2016).

2. Methods

2.1. Subjects

We tested a cohort of 78 Labrador retrievers (n=48; 23 F/25 M) and Labrador retriever X German Wire-haired pointer crosses (n=30, 19 female) from 15 different litters from a purpose-bred detection dog population at Auburn University's Canine Performance Sciences program. Details on this population's breeding, development, and training history have been previously described (Lazarowski et al., 2018). Briefly, all dogs were whelped and reared under identical conditions and experienced the same training regimen from birth through 12 months of age. At 3, 6, 10, and 12 months of age, dogs underwent performance evaluations. The evaluations consisted of trainers judging dogs' performance and behavior in a variety of situations designed to test dogs' detection abilities (see Lazarowski et al., 2018 for details on the evaluation procedures).

Evaluations consisted of 14 items pertaining to one of three behavioral domains: Performance, which included 7 behavioral characteristics related to searching and scent detection, Environmental Soundness, which included 6 behaviors related to dogs' reactions to novel and/or sudden stimuli in the environment, and one overall measure of Trainability (ease of learning new tasks). Each item scored during the evaluation was given a 1-5 rating (described in Lazarowski et al., 2018). At the completion of training at approximately 12 months, dogs were either kept as breeders or offered for service to various detection dog agencies. Purchase and rejection decisions were made independently by the customer who conducted their own evaluations of the dogs, and thus all dogs received an objective final outcome categorization depending on successful or unsuccessful sale. Canine Performance Sciences breeds and develops all dogs for the ultimate goal of being sold for *Vapor Wake*®, which is a specialized type of detection of airborne moving targets. Dogs capable of *Vapor Wake*® detection have been shown to possess unique, superior behavioral characteristics relative to standard detection dogs not suitable for *Vapor Wake*® (Lazarowski et al., 2018). Any dog not able to be sold for *Vapor Wake*® is presented for sale to other, lower-tier general explosives detection dog agencies, retained for odor discrimination research, or adopted as pets. Therefore, dogs from this population can be categorized in a rank-order according to their final outcome. For the purposes of our analyses in this paper, we used a binary variable to categorize dogs' final outcome as 'suitable' (successfully sold under the *Vapor Wake*® classification or retained as breeders) or 'unsuitable' (unable to be sold under the *Vapor Wake*® classification; this category included dogs sold for other purposes as well as dogs released from the training program).

Testing occurred when dogs were either approximately 3 months (n= 25; 13 female; mean age 3.61 mo), 6 months (n=27; 15 female; mean age 5.99 mo), or 11 months of age (n=26,

14 female; mean age 11.22 mo). For our purposes, we labeled the groups as puppies, juveniles, and adolescents, respectively. All dogs were intact at the time of testing except for 3 males and 2 females in the oldest test group. Age of testing was randomly assigned at birth, with 2-4 dogs from a given litter in each age group. In addition to these cross-sectional groups, six dogs from the puppy group were tested longitudinally at each age. Age of testing corresponded to the timing of training evaluations conducted by the program to allow for comparisons between task performance and training evaluation scores, as well as developmental differences.

2.3. Procedure

Methods were based on those of Passalacqua et al. (2011). The apparatus consisted of an 11x14x14 cm transparent storage container (Sterilite®, Townsend, MA, USA) with a removable and lockable lid. The lid was screwed, up-side down, to a 45-cm circular wooden board. The base of the container could be positioned over the lid and either left unlocked by leaving the latches unlocked or could be locked into place by securing the latches. Testing occurred in an empty treatment room inside the kennel building where the dogs resided.

The procedure consisted of a warmup trial to acclimate dogs to the apparatus, immediately followed by three consecutive solvable trials in which the container could be displaced from the base, followed by one unsolvable trial in which the container was locked to the lid. At the start of each trial, dogs were held at a fixed starting position 1 m from the apparatus. The experimenter called the dog's attention while holding the toy up for the dog to see, placed the toy on top of the lid, and covered the toy with the container. For the warmup trial, the container was loosely placed without completely covering the lid and could be easily knocked over. For the three solvable trials the container was secured onto the lid but was not locked into place, allowing it to be dislodged if manipulated. For the unsolvable trial the lid was

locked and secured to the container. On all trials, the dog was released after the experimenter arranged the apparatus according to the condition and stepped back to stand next to the handler. The experimenter and handler remained in the start position maintaining a neutral expression and orienting their gaze towards the apparatus. All trials lasted 1 min, or until the container was dislodged if applicable, whichever came first. All experimental activities were approved by the Auburn University Institutional Animal Care and Use Committee.

2.4. Behavioral scoring

Several dependent measures were scored from video. For the solvable condition (trials 1-3), latency in seconds from first contact with the apparatus until the toy was uncovered was recorded. For the unsolvable condition (trial 4), several task-oriented and human-directed behaviors were measured (see Table 2-1). Each session was scored from video by an independent observer, and a randomly selected subset (20%) for each group was additionally scored by a second independent observer to determine inter-rater reliability (Intra-class correlation coefficient: gaze experimenter duration ICC = .813; gaze apparatus duration ICC = .983; interact with experimenter duration ICC = .983; persistence duration ICC = .928; gaze alternation frequency ICC = 0.993).

2.5. Statistical analyses

Separate analyses were conducted for developmental effects and relationships between unsolvable task performance and working dog performance. Shapiro–Wilk tests revealed that the data were not normally distributed for any of the dependent measures for the 3, 6, and 11-mo groups ($p < .05$); therefore, non-parametric tests were used for analyses of developmental effects. Kruskal-Wallis H tests were performed to determine if there were differences between the three age groups for each dependent measure of the unsolvable task. Distributions of scores were

similar for all groups, as assessed by visual inspection of a boxplot. Pairwise comparisons were performed using Dunn's test with a Bonferroni correction for multiple comparisons. Adjusted *p*-values are presented.

Relationships between unsolvable task performance and working dog performance were determined by correlating each dog's dependent measures in the unsolvable task with scores from their performance evaluations. First, a principal component analysis (PCA) was run for data reduction of the 14 items in the evaluation. Because only the oldest group consistently received the acoustic and visual startle tests, we removed this factor prior to the PCA analysis. We recently analyzed the evaluation scores and their relevance to program outcome in a larger sample of 146 candidate detector dogs from this same population and found that two factors, retrieve and excitability, were not useful predictors of performance (Lazarowski et al., 2018). Thus, we also excluded these two factors from the PCA. Finally, because trainability is the only item in its category and therefore would not be expected to correlate with the measures of the other domains, we did not include it in the PCA. We then correlated the component scores of the PCs calculate by the PCA to the dependent measures of the unsolvable task using a Spearman rank-order correlation. Additionally, comparisons of unsolvable task performance between dogs categorized based on final program outcome were performed for each age group. Shapiro–Wilk tests revealed that the data were not normally distributed for the suitable and unsuitable groups ($p < .05$) for all dependent measures except latency to solve, persistence, and time away from apparatus in puppies, latency to give up in juveniles, and persistence in adolescents; therefore, independent samples *t*-tests were run to compare groups based on outcome for these measures, and non-parametric Kruskal-Wallis H tests were performed for the rest. Mann-Whitney U tests were performed to determine if there were differences in unsolvable task performance between

dogs categorized according to final program outcome. Distributions of scores were similar for all groups, as assessed by visual inspection of a boxplot.

All statistical analyses were performed using SPSS. Due to camera malfunction, data from one puppy was not included in the analyses and only partial data (solvable trials) from one 11-month old dog was used. Two dogs were deemed medically ineligible for sale before completing training and did not receive a final outcome corresponding to sale status, and therefore were not included in some of the analyses.

3. Results

3.1. Developmental effects

3.1.2. Human-directed behaviors

Figure 1-1 shows between-group age differences for median percentage of trial time interacting with the experimenter, ($\chi^2[2] = 22.992, p < .001$), and gazing at the experimenter, ($\chi^2[2] = 27.091, p < .001$). Post hoc analyses revealed less interaction with the experimenter between adolescents and both other groups, (p 's $< .021$) but no difference between puppies and juveniles ($p = .082$). Percentage of trial time spent gazing at the experimenter was higher adolescents compared to puppies ($p < .001$) and juveniles ($p < .001$), (Fig 1-1). Frequency of gaze alternations was also different between groups, ($\chi^2[2] = 26.205, p < .001$), with adolescents gaze-alternating between the experimenter and the apparatus more frequently than puppies ($p < .001$) and adolescents ($p < .001$).

3.1.3. Task-oriented behaviors

Figure 1-1 also shows between-group differences for percentage of time gazing at the apparatus, $\chi^2(2) = 44.785, p < .001$. Adolescents gazed at the apparatus significantly more than both juveniles ($p < .001$) olds and puppies ($p < .001$).

Percentage of time spent away from the apparatus also significantly differed between groups, $\chi^2(2) = 6.045, p = .049$ (Fig 1-1). However, adjusted post-hoc comparisons did not show any significant differences. No statistically significant differences were found for latency to open the container during the solvable trials, $\chi^2(2) = 1.848, p = .397$, latency to give up during the unsolvable trial, $\chi^2(2) = 14.797, p = .091$, or persistence, $\chi^2(2) = 5.004, p = .082$.

3.2. Relationship to working dog performance

3.2.1 Correlations between unsolvable task performance and detection dog evaluations

The suitability of PCA was assessed prior to analysis. The correlation matrix showed that all variables had at least one correlation coefficient greater than 0.3. The overall Kaiser-Meyer-Olkin measure was 0.87 with individual KMO measures all greater than 0.7, and Bartlett's Test of Sphericity was statistically significant ($p < .001$). Therefore, a PCA was considered appropriate.

The PCA revealed two components that had eigenvalues > 1 , which explained 59.49% and 21.01% of the total variance, respectively. Visual inspection of the scree plot indicated that three components could be retained, and a two-component solution met the interpretability criterion. Therefore, we decided to retain two components for further analysis, which together explained 80.476% of the total variance. A Varimax orthogonal rotation was applied, which exhibited 'simple structure'. The interpretation of the data was consistent with the domains used to categorize the items in the evaluation (Lazarowski et al., 2018). Items related to dogs' ability to perform scent detection tasks, which all pertained to the 'Performance' domain of the evaluation, loaded strongly onto Component 1 which was therefore labeled Performance. Items related to dogs' reactions to novel people and stimuli in the environment, which all corresponded to the 'Environmental Soundness' domain of the evaluation, loaded onto Component 2 which

was therefore labeled Environmental Soundness. Component loadings and communalities of the rotated solution are presented in the Appendix.

The component scores for each subject calculated by the PCA, as well as Trainability scores, were then correlated with each dependent measure of the unsolvable task. The Performance component score showed weak but significant correlations with interaction with the experimenter, $r_s(71) = -.324, p < .001$, frequency of gaze alternations, $r_s(71) = -.310, p < .001$, and gazing at the apparatus, $r_s(71) = .315, p < .001$. The Environmental Soundness component score showed a weak but significant negative correlation with average latency to solve, $r_s(72) = -.293, p < .05$. The Trainability component score showed weak but significant correlations with frequency of gaze alternations, $r_s(71) = .265, p < .05$, and time away from the apparatus, $r_s(71) = -.238, p < .001$.

3.2.2. Unsolvable task performance by program outcome

In puppies, suitable dogs had shorter latencies to solve the task than unsuitable dogs ($t[14] = -2.38, p = .032$). No other measures differed between groups at these ages.

Figure 1-2 shows that in adolescents, suitable dogs were higher than unsuitable dogs in percentage of trial time spent gazing at the experimenter (Mann-Whitney U test: $U = 144.5, p < .001$) and at the apparatus (Mann-Whitney U test: $U = 125, p < .010$). Suitable dogs also had higher frequency of gaze alternations (Mann-Whitney U test: $U = 153, p < .001$), and shorter latencies to give up (Mann-Whitney U test: $U = 37.5, p < .026$). There were no significant differences for latency to solve (Mann-Whitney U test: $U = 91.5, p = .699$), interaction with the experimenter (Mann-Whitney U test: $U = 59, p = .139$), or persistence ($t[20.13] = -1.071, p = .297$).

4. Discussion

The goal of the current study was to assess developmental effects of age and experience on both human-directed communicative behavior and task-oriented persistence in an unsolvable task in dogs bred and trained for scent detection, and to identify potential relationships between unsolvable task performance and working dog suitability. To our knowledge, this is the first study to utilize the unsolvable task with respect to working dog development and performance. We found that, consistent with one other study evaluating developmental effects in the unsolvable task in dogs (Passalacqua et al., 2011), the oldest group gazed at the apparatus for greater portions of the unsolvable trial than the younger groups, but we did not find any significant age differences in persistence. Similarly, and again in alignment with findings from Passalacqua et al. (2011), human-directed communicative behavior (e.g., gaze alternation) increased with age. Gaze alternation has also been shown to increase with age in feral dogs in an object-choice task (Bhattacharjee et al., 2017). The adolescent group in our study gazed at the human for greater portions of the unsolvable trial than younger puppies, and the same pattern was seen in frequency of gaze alternations which is considered a stronger indication of joint attention and intentional communication (Miklósi et al., 2000; Passalacqua et al., 2011). This finding echoes evidence of the developmental trajectory of gaze alternation in non-human primates, and contrasts that of human children who begin to produce gaze alternations early in development (Lucca et al., 2017). However, we found negligible durations and frequencies of human-directed gazing and gaze alternations in the two youngest groups relative to similar age groups in Passalacqua et al. (2011). Although we did not directly compare detection dogs to pets in our study, this contrast suggests that human-directed gazing emerges at a younger age in pet dogs than in detection dogs, which may be a product of training. For example, detection dogs

begin training at a very young age to work independently and to ignore people. In operational settings, detection dogs must be able to maintain focus while searching and not be distracted by people, including distractions from people in public areas as well as unintentional handler cueing (Minhinnick et al., 2017). While detection dogs' reduced opportunities for incidental learning about communicating with humans through daily interactions due to rearing and housing environments could be a factor, puppies in the Passalacqua et al. (2011) study lived with their litter in pens and not in human homes and had restricted human interaction. Thus, differences are not likely due to conditioning via human interaction experienced in daily life. However, without directly comparing these populations and controlling for other factors, it is not clear whether these differences are attributable to differences in rearing environment, training, genetics, or potential methodological differences. These findings support the hypothesis that human-directed communicative behavior is a learned behavior resulting from experience and interactions with humans during development (Passalacqua et al., 2011).

Another possible explanation for the increase in human-directed gazing with age is that training in general may increase human-directed gazing by inadvertently reinforcing attention to the trainer. This interpretation is consistent with reports that dogs trained for sport and working roles including agility, search and rescue, and water rescue gazed more at a human during the unsolvable task than untrained pets (D'Aniello et al., 2015; Marshall-Pescini et al., 2009). Increases in gazing at the apparatus with age may also be a product of training. Specifically, explosives detection dogs are typically trained to give a "passive" response, meaning dogs alert to a target odor by giving some kind of behavior signal (e.g., sitting, lying down) at a safe distance from the target and physical contact with the target is explicitly prohibited for obvious safety reasons. Additionally, training often involves building an uninterrupted, sustained stare at

the target to demonstrate the dog's focus. Thus, adolescents in our study who were more advanced in their detection training than younger dogs, who had not yet received any odor discrimination training yet, may be generalizing trained responses to the unsolvable task. Indeed, authors have suggested that the use of human-directed gazing in different populations of canids may serve varying, context-dependent functions (Brubaker et al., 2017).

Another aim of this study was to determine relationships between unsolvable task behaviors and working dog performance as assessed by trainer evaluations. To do so, we correlated durations and frequencies of human-directed and task-oriented behaviors during the unsolvable task with component scores determined by the PCA of trainer-rated evaluations of dogs' performance on a number of detection dog measures. Significant correlations were found between unsolvable task behaviors, both task-related and human-directed, and detection dog performance measures. A significant positive correlation was found between frequency of gaze alternations and trainability. This is contrary to our prediction that successful detection dogs would display low levels of human-directed behavior due to training for independence, and may suggest the importance of cooperation and communication with people in a dogs' ability to be trained regardless of the nature of the work. This relates to recent findings that oxytocin, which is mediated by gazing between dogs and humans, is associated with trainability in detection dogs (Konno et al. 2018). Additionally, gaze alternations positively correlated with dogs' Performance component scores, which may be due to dogs' underlying motivation. That is, dogs that are strongly motivated to work and exhibit higher "drive" are likely to exhibit stronger characteristics related to searching and other detection tasks. These same dogs are also more likely to be highly motivated to obtain the toy in the unsolvable task, looking to the human as an alternate strategy when persisting proves unproductive. However, we found a significant

negative correlation between percentage of time interacting with the experimenter and Performance component scores, suggesting that dogs' ability to utilize human-directed gazing functions as a goal-directed behavior but that interacting with people may be indicative of dogs' distractibility. Thus, it appears that there may be an optimal level of human engagement necessary for successful training.

Performance component scores also positively correlated with percentage of time spent gazing at the box, further indicating the role of motivation for the reward in unsolvable task performance. The only unsolvable task measure to correlate with Environmental Soundness component scores was average latency to solve during the solvable trials. This is likely explained by neophobia and boldness, in that dogs' willingness to approach and manipulate the apparatus may have modulated their speed to solve the task. More fearful dogs may have been hesitant to approach and interact with the apparatus, which would have improved their speed of solving the task. Future research including other measures of dogs' behavior during the unsolvable task such as exploratory behavior and indications of fear and anxiety may clarify the relationship between boldness/neophobia and persistence.

We also analyzed unsolvable task behaviors at each age as a function of final program outcome (i.e., successful or unsuccessful placement as a VaporWake® dog) in order to determine whether unsolvable task performance was predictive of successful program outcome and if so, how early these indications emerged. In puppies, suitable dogs had faster latencies to solve the task than unsuitable dogs. At 11 months of age, significant differences emerged in both human-directed communicative behaviors and task-related behaviors with suitable dogs gazing more to both the human and the apparatus. However, suitable dogs had shorter latencies to give up than unsuitable dogs, but this may be a product of their increased time gazing at the human

and apparatus, or, as discussed, a carry-over effect of training to not aggress targets. Overall, we found evidence that detection dogs' unsolvable task performance relates to their performance and success in working contexts, with some indications of future performance becoming apparent as young as 3 months old.

These findings only partially supported our predictions that greater independence and persistence in the unsolvable task would be associated with detection dog success. While successful dogs gazed longer at the apparatus, which may reflect greater motivation for the reward than unsuccessful dogs, they also utilized human-directed communicative gazing more, which was opposite to our prediction. It appears that despite the notion that handler-dependent detection dogs are undesirable, some degree of engagement with people is important. In fact, in a survey of handler and trainer ratings of important attributes for successful detection dogs, *obedience to commands* and *willingness to bring an object back to a person* were rated as highly important (Rooney et al., 2004). As discussed, attention to and engagement with people is likely important for a dogs' trainability. While independence is important for detection dogs' resistance to human-cueing and biasing and has been shown to predict success in some types of working dogs (Diverio et al., 2016), too much independence may lead to dogs that are unresponsive and therefore untrainable. Given that training requires attending to human commands and signals and a great part of dog training utilizes praise and social play with the trainer as reinforcement, this is not surprising. Indeed, factors related to the handler-dog dynamic including cooperation and communication has been considered as important as the dog's physical and behavioral characteristics (Diverio et al., 2017). Future research is needed to determine to what extent a detection dog needs to be engaged with humans and whether there is an optimal level before a dog becomes overly reliant to the point that it interferes with the ability to work independently.

Other measures of social cognition that have been extensively utilized in the canine cognition literature with respect to investigating the dog-human bond and the origins of canine cognition, such as point-following, emotion discrimination, and emotion contagion, may be useful for exploring this question.

A limitation of this study is that our results may be specific to this population and the characteristics and behavioral repertoire necessary for dogs capable of VaporWake® detection, and not necessarily applicable to other types of detection and working dogs. Indeed, we previously found that the behavioral characteristics possessed by VaporWake® suitable dogs are distinct from those of standard explosives detection dogs (Lazarowski et al., 2018). Thus, future research is needed to determine the relationship between unsolvable task performance and success in dogs bred and trained for different roles. Another potential limitation is the use of sale status to determine a dog's so-called success. Purchase decisions could be subject to the ebb and flow of supply and demand, which could influence an individual dog's categorization. Different agencies may also vary in evaluation methods and standards of acceptance. This only underscores the critical need for universal standardization of the parameters used to characterize different working dog characteristics.

5. Conclusions

The results of the present study add to the growing body of literature suggesting that, while dogs may have developed a genetic predisposition to attend to and interact with humans throughout the process of domestication, additional experience with humans is necessary for dogs to learn to utilize human-directed problem-solving strategies. Our results also indicate that the contexts in which dogs interact with humans, and potentially different types of training, may affect the emergence of such behaviors. Additionally, our findings that persistence and human-directed

behaviors on the unsolvable task relate to and predict detection dog performance and outcomes as early as 3 months old has implications for improving current working dog selection methods.

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Condition	Category	Measure	Scale	Definition
Solvable	task-oriented	latency to solve	duration (s)	first contact with apparatus until toy is uncovered (average)
Unsolvable	task-oriented	persistence	percentage of time	physical contact with apparatus
		gaze at apparatus	percentage of time	from stationary position, dog orients gaze towards apparatus
		latency to give up	duration (s)	first contact with apparatus until dog ceases interacting
	human-directed	time away	percentage of time	dog is engaged in other behavior, oriented away from apparatus
		interaction with experimenter	percentage of time	physical contact with experimenter
		gaze at experimenter	percentage of time	from stationary position, orients gaze towards experimenter

Table 2-1. Behavioral ethogram used to score behaviors during the unsolvable task.

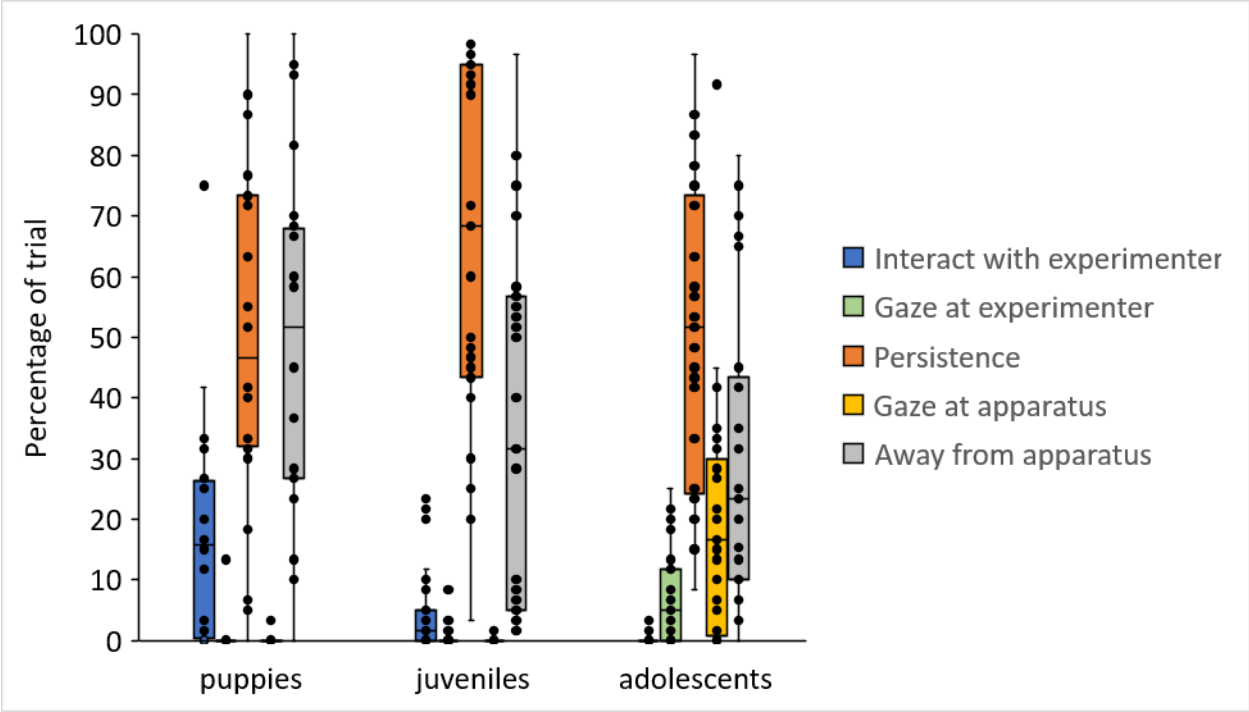


Figure 2-1. Distribution of human-directed and task-oriented behaviors during the unsolvable trial as a function of age.

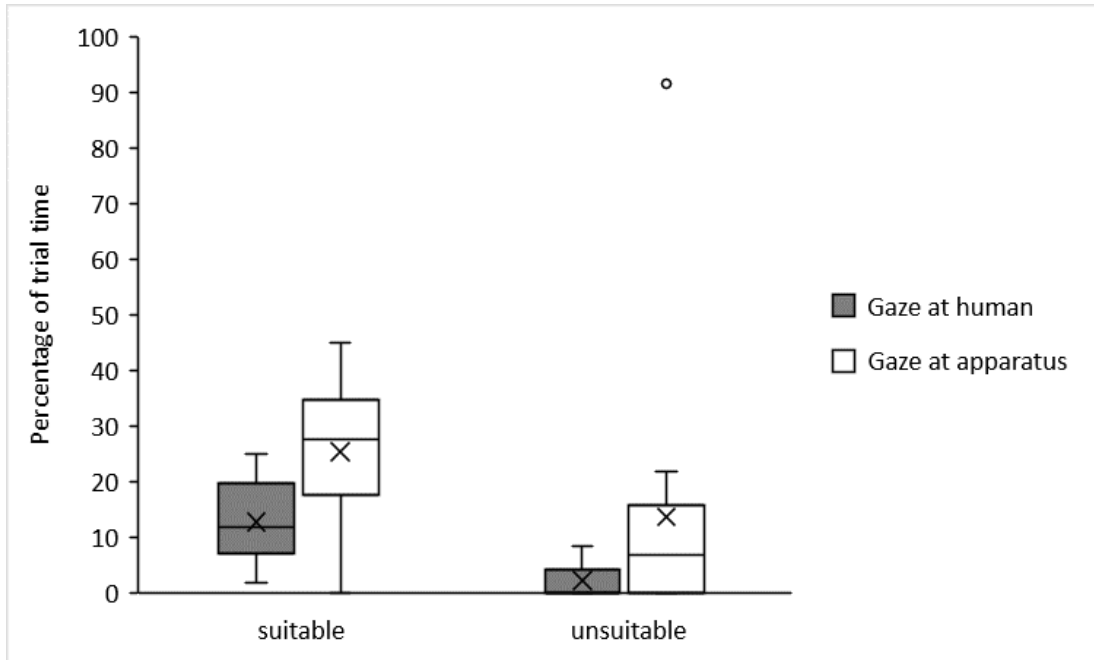


Figure 2-2. Percentage of trial time spent gazing at the human and the apparatus in adolescents as a function of program outcome.

Chapter III: Ontogenetic effects on responsiveness to social and olfactory cues in detection

dogs

Abstract

Dogs are highly responsive to human communicative gestures and will readily follow gestures, such as pointing, to locate hidden rewards. Dogs' reliance on human social signals is so strong that they will follow misleading cues despite directly contradicting perceptual information. However, this bias likely reflects dogs' enculturation with humans and reports may not be representative of other populations of dogs. This study investigated preference for social versus physical cues in a cohort of candidate detection dogs explicitly trained to ignore irrelevant human cues and selectively attend to olfactory information. We found that opposite to previous findings, responsiveness to human pointing decreased with age while the ability to locate the reward by scent increased. Further, susceptibility to social cues was predictive of detection dog placement failure. These findings further establish the influence of ontogenetic effects on social cognition, and demonstrate potential applications for early identification of suitable detection dogs.

Introduction

Extensive research has established that dogs are capable of flexibly responding to human-communicative signals (Kaminski & Nitzschner, 2013; Reid, 2009). The object-choice task has been widely used to investigate these abilities, in which a reward is hidden in one of two or more locations and dogs are presented with a human signal to indicate the reward's location.

Approaching the location indicated by the human's gesture is interpreted as an understanding of the communicative intent behind the signal. Using this task, dogs have been shown to be capable

of responding to a variety of human gestures including pointing using arms or legs (Lakatos et al., 2009; Miklósi & Soproni, 2006), bowing (Agnetta et al., 2000), nodding (Soproni et al., 2001), head turning (McKinley & Sambrook, 2000), and gazing (Miklósi et al., 1998).

Dogs' high levels of performance on the object-choice task contrasts with poor performance in this task by non-human primates (Hare & Tomasello, 2005). This finding that dogs appear to demonstrate superior communicative abilities with humans than our closest ancestors led to the hypotheses that dogs' socio-communicative abilities evolved during domestication via selection for attention and responsiveness to human social signals (Hare et al., 2010). This hypothesis was further supported by comparisons of domestic dogs' object-choice task performance with *their* closest wild ancestors, wolves (*Canis lupus*), which again demonstrated superior abilities in dogs (Hare et al., 2002). However, follow-up studies with human-socialized wolves have demonstrated that differences in developmental periods and corresponding socialization with humans mitigates these dog-wolf differences (Udell et al., 2010). Consequently, over a decade of investigations of the socio-cognitive abilities of species differing in domestication and socialization status including kenneled (D'Aniello et al., 2017; Lazarowski & Dorman, 2015; Udell et al., 2010) and free-ranging dogs (Bhattacharjee et al., 2017), ungulates (goats: Kaminski et al., 2005; horses: Maros et al., 2008; pigs: Nawroth et al., 2013; elephants: Smet & Byrne, 2013), ferrets (Hernádi et al., 2012), marine mammals (dolphins: Herman et al., 1999; sea lions: Malassis & Delfrour, 2015; fur seals: Scheumann & Call, 2004), and non-human primates (capuchins: Anderson et al., 1995; orangutans: Call & Tomasello, 1994; macaques: Schmitt et al., 2014), have led to numerous hypotheses regarding the relative roles of both genetic history and experience in the comprehension of human gestures (Udell et al., 2010; Udell & Wynne, 2010).

Taken together, evidence suggests that dogs' ability to understand and utilize human communicative cues stems from a genetically predisposed heightened sensitivity and attention to humans, the development of attachment bonds to humans during critical socialization periods, and conditioning to human actions via daily activities (Udell & Wynne, 2010). These phylogenic and ontogenetic advantages are at the root of dogs' ability to integrate into human society in ways unlike any other species. In addition to utilizing human gestures, dogs' so-called 'human-like' socio-cognitive abilities have enabled more complex social competencies such as sensitivity to human emotional and attentional states (Call et al., 2003; Müller et al., 2015), imitation of human actions (Fugazza et al., 2017; Pongrácz et al., 2005), and discrimination of human voices (Adachi et al., 2007). However, a potential cost to this social advantage is that modern dogs appear to be so strongly biased towards humans that non-social problem-solving skills are stunted. This may be the result of domestication, in which selection for attraction to humans also selected against independent problem-solving skills, or the ontogenetic development of a dependence on humans due to the lack of any ecological challenges faced by pet dogs living in human homes. For example, dogs perform poorly in locating hidden rewards based on causal visual and auditory cues whereas non-human primates are much more successful (Bräuer et al., 2006), and commit the Piagetian 'A-not-B' error only when there is human involvement, whereas wolves are not affected in this way (Topál et al., 2009). Dogs' bias towards humans is so strong that they will even rely on human-provided cues that are misleading, conflict with direct perceptual information, or lead to suboptimal choice (Marshall-Pescini et al., 2011; Prato-Previde et al., 2008; Szeteci et al., 2003; Takaoka et al., 2014).

Szeteci et al. (2003) demonstrated the potency of dogs' bias towards human social signals by presenting dogs with conflicting social and perceptual cues regarding the location of hidden

food. Using a two-way object-choice task, dogs were given a choice between an empty container signaled by a human pointing, versus a container baited with food in which the dogs were allowed to smell its contents prior to making a choice. Despite direct physical information about the location of the food, dogs tended to follow the misleading human pointing cue. This result is surprising given dogs' superior olfactory abilities (Goldblatt, 2009), but further demonstrates the influence of humans on dog behavior and cognition.

A noteworthy limitation in the body of research regarding the extents and limits of canine cognition is that of a sampling bias, in which the majority of these studies use pet dogs. Many conclusions about the origins of dogs' cognitive abilities are based on this population, which seems shortsighted given what we know about the effects of experience on the development of socio-cognitive skills. Working dogs starkly contrast pet dogs in their life histories and daily activities, and therefore may provide an important comparison to pet dogs for studies on canine cognition. Scent detection dogs, for example, are required to work independently and not be influenced by extraneous stimuli, including unintentional cueing from people. Detection dogs that are handler-dependent are considered problematic, and dogs are typically explicitly trained *not* to be biased by human cues (Helton, 2009; Lit et al., 2011). In fact, in advanced detection training distracting stimuli such as the trainer's body orientation or vocalizations are introduced as intentionally conflicting cues that dogs must ignore while working. A successful detection dog is one that can work past irrelevant and potentially incorrect sources of information and loyally follow their nose. Previous research has shown that in an explosives search scenario, trained detection dogs default to using their olfactory sense rather than vision to locate explosives even when visual cues are more readily accessible (Gazit & Terkel, 2003), but handler beliefs about the location of target odors can unintentionally cue a dog to give a false alert in the absence of a

target odor (Lit et al., 2011). However, to our knowledge no studies have directly pitted olfactory versus social cues to determine sensory bias in detection dogs. Evaluating responsiveness to human cues in detection dogs, especially when in conflict with olfactory information, may have several implications. Assessing the development of cue-following in a population of dogs with vastly different life histories than pet dogs, especially in regard to exposure to human social stimuli, may provide further insights in the continuing debate regarding the origins of dogs' responsiveness to human communicative cues. Second, measures of dogs' susceptibility to human influence in deference to available olfactory information may be useful in identifying dogs that are prone to handler cueing and bias. This latter point has potential applications to the working dog industry, potentially providing a useful selection method for identifying suitable versus unsuitable dogs for working roles. Therefore, in this study we sought to further explore dogs' tendency to be misled by human cues that conflict with sensory information, namely olfactory cues, in a population of candidate scent-detection dogs. Specifically, we tested dogs on the widely used object-choice task to determine their preference in following a human pointing gesture versus the scent of a reward. Dogs were tested at three different ages across early development in order to determine ontogenetic effects of cue-following in detection dogs, as well as whether dogs' biases towards particular cues were predictive of future success as a detection dog. We predicted that, unlike pet dogs as in Szetei et al. (2003), detection dogs would not be biased towards misleading human signals that conflict with olfactory cues due to 1) limited experience and conditioning to human gestures compared to pets and 2) explicit training to ignore irrelevant human cues and attend only to olfactory information. Second, we hypothesized that detection dogs' preference for human or olfactory cues would be indicative of their potential as a successful detection dog.

Methods

Subjects

A total of 75 Labrador retriever and Labrador retriever crosses from a purpose-bred detection dog breeding and development program were tested. All dogs were born and reared in the same environment, and experienced the same socialization, development, and training program from birth through approximately 12 months old (see Lazarowski et al., 2018 for further details on this population). At the completion of the training program, dogs were categorized based on their ultimate successful or unsuccessful placement in service. Categorization was based on the dog's sale status (i.e., purchased or rejected), which was decided by third-party customers who conducted independent evaluations. Thus, we categorized dogs as “successful”, which included dogs retained for breeding as well as dogs sold to any agency for detection service, or “unsuccessful”, which included dogs not able to be sold for detection work (i.e., dogs that were re-purposed for other non-detection activities or were adopted out of the program).

We tested dogs corresponding to three different age groups: puppies (n=24, mean age 3.33 mo), juveniles (n=27, mean age 5.42 mo), and adolescents (n=24, mean age 11.38 mo). These ages were chosen to correspond with the ages at which the program conducted behavioral evaluations of the dogs' detection performance (described below). Testing occurred within one week of the evaluations.

Procedure

Pre-training

In order to familiarize the dogs with the test setup and learn that toys could be found in the containers, two pre-training trials were conducted prior to the experimental trials. Two identical opaque containers were positioned 1 m away on either side of the experimenter while

the dog was held 1.5 m away facing the experimenter. The experimenter called the dog's name, held up a toy, and placed it in one of the two containers. When the experimenter returned to the start position the dog was released to retrieve the toy. If the empty container was approached first, the experimenter led the dog to the correct location and allowed the dog to retrieve the toy. The same procedure was then repeated on the other side, with the order of the first rewarded location randomized for each dog.

Testing

Experimental trials involved a two-way choice procedure using a similar procedure to that of Szetei et al. (2003). We chose to use toys as the reward, which are exclusively used as the dogs' reward during training. Toys used in the task matched those that were used in the dogs' training, and differed depending on the dogs' age. For the younger puppies and juveniles, we used soft fleece toys, KONG® Wubbas, and KONG® Squeezz Jels. The particular choice of toy for each puppy was based on the dog's initial interest in the toy prior to beginning the experiment. If the puppy did not show interest in a toy (e.g., did not chase, retrieve, or pick up the toy on first presentation), a different toy was selected until the dog showed interest. Puppy toy preferences were often influenced by teething, therefore both hard and soft toys were offered. For the oldest group, a Chuck It!® Ultra ball was used.

Two people participated in the task: the experimenter, who arranged the stimuli and displayed the cues, and the handler, who handled the dog throughout the session. On each trial, the experimenter stood equidistantly in between two containers placed .5 m away on either side (Fig 3-1), and remained at this location for the duration of the trial. The containers were identical in appearance, opaque with perforated lids measuring (dimensions). The container designated as the positive stimulus (S+) was pre-baited with a toy before each trial, out of the dog's view,

while the other (S-) remained empty. In order to minimize cross-contamination of odor cues, the same container was always used as the S+. Dogs began each trial at the start position approximately 1.5 m in front of the experimenter. At the start of each trial, the handler walked the dog on leash to the container on the dog's right, allowed the dog to sniff the container for 2 seconds, and then repeated the action with the container on the dog's left after which the handler returned the dog to the starting position. Once the handler and dog returned to the start position, the experimenter called the dog's name and pointed to the S- container using the ipsilateral arm while simultaneously looking at the container. The dog was then released and allowed 15 s to make a choice, defined as any part of the head coming within a 10-cm radius of either container. The experimenter held the point until the end of the trial. If the dog chose the correct container (S+), the experimenter opened it and rewarded the dog with the toy and social praise. If the dog chose the S- (i.e., the container that the experimenter pointed to), the experimenter opened the container and showed the dog that it was empty. After either a choice was made or 15 s lapsed without any choice, the dog was returned to the start position for the next trial to begin. A total of 10 trials were conducted, with the location of the toy counterbalanced across trials so that the S+ appeared on the left and right sides an equal number of times, with the constraint that the same side not be baited for more than two consecutive trials.

Scoring and data analysis

Three scores were calculated for each dog: percentage of total trials in which the baited container was chosen, percentage of total trials in which the [empty] container to which the experimenter pointed was chosen, and percentage of total trials in which neither container was chosen within 15 s.

Developmental differences in responsiveness to social and olfactory cues were assessed by comparing each score between age groups. Shapiro–Wilk tests revealed that the data were normally distributed for both cue types for all age groups ($p > .05$), but not for non-responses. Therefore, a one-way ANOVA was conducted for analyzing age differences for the two cues, and a non-parametric (Mann-Whitney U) test was used to analyze age differences in non-responses.

To determine relationships between responsiveness to the different cues and working dog performance, scores for each cue were correlated to trainer-rated scores of the dogs' behavioral evaluations assessed during the routine program evaluations. Evaluations consisted of subjective trainer-assessed ratings of 14 characteristics on a 1-5 scale (see Lazarowski et al., 2018 for more details on the evaluation and scoring). We previously performed a principal component analysis (PCA) which found two principal components of Performance (behavioral characteristics related to searching abilities) and Environmental Soundness (reactivity to novel stimuli in the environment). For the current analysis, we used a Spearman's correlation to correlate component scores calculated from the PCA to scores in the current task.

Finally, to determine whether task performance was predictive of dogs' success as a detection dog, we analyzed scores from the current task as a function of outcome categorization (i.e., successfully or unsuccessfully placed in service).

Each session was live-scored by the experimenter. A subset (20%) of sessions were additionally double-scored from video by an independent observer in order to determine Cohen's kappa for inter-rater reliability. Agreement between the two scorers was very good, $k = .883$, $p < .001$.

Results

Developmental effects

A one-way ANOVA was conducted to analyze effects of age on cue-following. Figure 3-2 shows allocation of responses as a function of age. Percentage of correct responses (choosing S+) was significantly different between age groups, $F(2, 72) = 8.944, p < .001$. Tukey post hoc analysis revealed that the mean increase in percent correct between puppies and adolescents was statistically significant ($p = .002$), as was the increase from juveniles to adolescents ($p = .001$), but the difference between puppies and juveniles was not statistically significant ($p = .99$). Both puppies and juveniles were significantly below chance in accuracy as a group, $t(23) = -2.145, p = .043$, and $t(26) = -2.243, p = .034$, respectively. Adolescents were significantly above chance, $t(23) = 2.747, p = .011$. At the individual level, one puppy, no juveniles, and six adolescents chose the correct container significantly more than chance (at least 8/10 choices, binomial test, $ps < .043$).

Percentage of pointing cues followed was also significantly different between age groups, $F(2, 72) = 5.297, p = .007$. Tukey post hoc analysis revealed that the mean decrease in points followed from puppies to adolescents was statistically significant ($p = .01$), as well as the decrease from juveniles to adolescents ($p = .027$), but the difference between puppies and juveniles was not statistically significant ($p = .910$) (Fig 3-2). As a group, adolescents were significantly below chance in point-following, $t(23) = -3.609, p = .001$. At the individual level, two puppies, four juveniles, and one adolescent were significantly above chance in point-following, (at least 8/10 choices, binomial test, $ps < .043$).

Percentage of no-choice trials did not differ as a function of age, $\chi^2(2) = 3.794, p = .150$.

Relationships to detection dog performance

Percent correct was positively correlated with component scores for Performance, $r_s(72) = .315, p = .006$, and Trainability scores, $r_s(72) = .342, p = .003$. Percentage of pointing cues followed was negatively correlated with component scores for Performance, $r_s(72) = -.246, p = .035$, and Trainability scores, $r_s(72) = -.273, p = .018$. Percentage of non-response trials did not correlate with any of the component scores.

Performance by neither of the two younger groups differed from chance as a function of outcome, for either of the two cues. Fig 3-3 shows allocation of responses for each cue in the oldest group as a function of outcome; successful dogs' mean percent correct (i.e., choosing the baited container) was greater than chance, $t(14) = 3.286, p = .005$. As there were no non-responses by this group, mean percentage of choices to the empty/human-cued container was proportionally below chance, $t(14) = -3.286, p = .005$. In the unsuccessful group, percentage of correct choices did not differ from chance $t(8) = .5, p = .631$, nor did percentage of points followed, $t(8) = -1.604, p = .147$. Three dogs in this group failed to respond on at least one trial.

Discussion

The current study investigated detection dogs' susceptibility to social influence when presented with human cues (i.e., pointing) that conflict with direct perceptual information (i.e., odor). Specifically, we assessed cue bias as a function of age in a population of detection dogs with unique life experience, relative to that of pet dogs generally studied in the literature, in order to further determine the effects of development and experience in domestic dogs' problem-solving skills. Further, we also examined whether detection dogs' bias towards humans versus odor cues would be a valuable predictor of successful or unsuccessful performance as a detection dog.

In order to assess developmental effects, we used a procedure similar to Szetei et al. (2003) of presenting dogs with conflicting social and olfactory cues in puppies, juveniles, and adolescents. Contrary to a large body of research indicating that point-following in dogs appears early in development and increases with age (Riedel et al., 2008; Wynne et al., 2008; Zaine et al., 2015), we found that puppies did not follow human pointing above chance levels, with further decreases as a function of age. In turn, dogs' ability to correctly locate the reward using olfactory cues increased with age. Though the patterns of responding that we found directly contrast previous findings showing increases with age, the effects we found are likely due to the specific environment and training of detection dogs. For example, although detection dogs receive intensive socialization with people and interact with trainers on a daily basis, they are typically reared with their litters and housed in kennel environments. Thus, opportunities for conditioning to human gestures through daily interactions with people are limited compared to that of pets residing in human homes and experiencing more encultured lifestyles. Other studies reporting poor point-following performance in kennel-reared dogs support this notion that environment plays a crucial role (D'Aniello et al., 2017; Lazarowski & Dorman, 2015; Udell et al., 2010). In the case of detection dogs, explicit breeding and training for scent-detecting abilities as well as resistance to human biasing likely further diminishes point-following tendencies and enhances scent-following. Furthermore, these results demonstrate that training and experience can overshadow reported breed differences in sensitivity to humans in dogs bred to work cooperatively with people (Dorey et al., 2009; Udell et al., 2014; Wobber et al., 2009). Thus, despite contrasting directions of results in our study compared to others, our findings nonetheless support hypotheses that experience greatly influences point-following in dogs.

Another possible explanation for the increase in correct choices (i.e., choosing the baited, “smelly” container) with age may be differences in working memory function. In the current experimental setup, dogs sniffed each container, returned to the start position, and then were released to make a choice while the experimenter pointed to the incorrect container. Because we used a static point, this cue remained visible throughout the trial whereas the odor cue was only briefly presented during the sniffing, introducing a short delay from the presentation of the odor cue and the time to make a choice. Given age-related differences in the development of attentional systems and working memory in human infants (Reynolds & Romano, 2016), it is possible that younger puppies had more difficulty maintaining attention and remembering where they had sniffed the correct container. However, no studies have investigated the early development of working memory in dogs, so the timing of the development of these processes is unknown. Though we intended to allow for the odor to be perceptible throughout the trial by perforating the lid and always using the same container for the S+, therefore removing the memory component, age-related differences in morphological and sensory systems, such as developmental increases in olfactory bulb and mitral cell size, may have caused age differences in the ability to smell the reward from a distance (Qin-guo et al., 2008).

Given the potential detrimental influence of human cueing on detection dog performance and the importance of deference to odor (Minhinnick et al., 2017), we also sought to investigate the relationship between social bias and detection dog performance. We found that dogs’ accuracy in choosing the baited container despite conflicting social cues correlated with trainer-rated composite scores reflecting dogs’ detection-related performance and trainability. That is, dogs that tended to choose the baited container and ignore social cues were more successful in their performance as a detection dog in working scenarios. On the other hand, dogs’ tendency to

be biased by human cues despite direct conflicting perceptual information was negatively correlated with their trainer-rated performance and trainability characteristics. That is, dogs showing susceptibility to human social influence tended to be weaker performers in detection dog working scenarios. We also investigated whether susceptibility to social influence was predictive of dogs' final placement after the completion of training, i.e., whether or not they were successfully placed in service or not. No predictive differences were apparent in younger dogs, but the oldest group showed differential performance between successful and unsuccessful dogs. We found that dogs' ability to locate the reward using odor cues and ignore human cueing was predictive of successful placement as a detection dog; specifically, dogs that were eventually placed in service as detection dogs had above-chance performance in utilizing odor cues and were below-chance in following pointing cues, whereas dogs that failed to be placed in service did not show selective preference for odor cues. Given challenges faced by the working dog industry regarding a lack of objective and predictive measures of success, our results suggest the potential utility in adopting cognitive assessments for improving selection.

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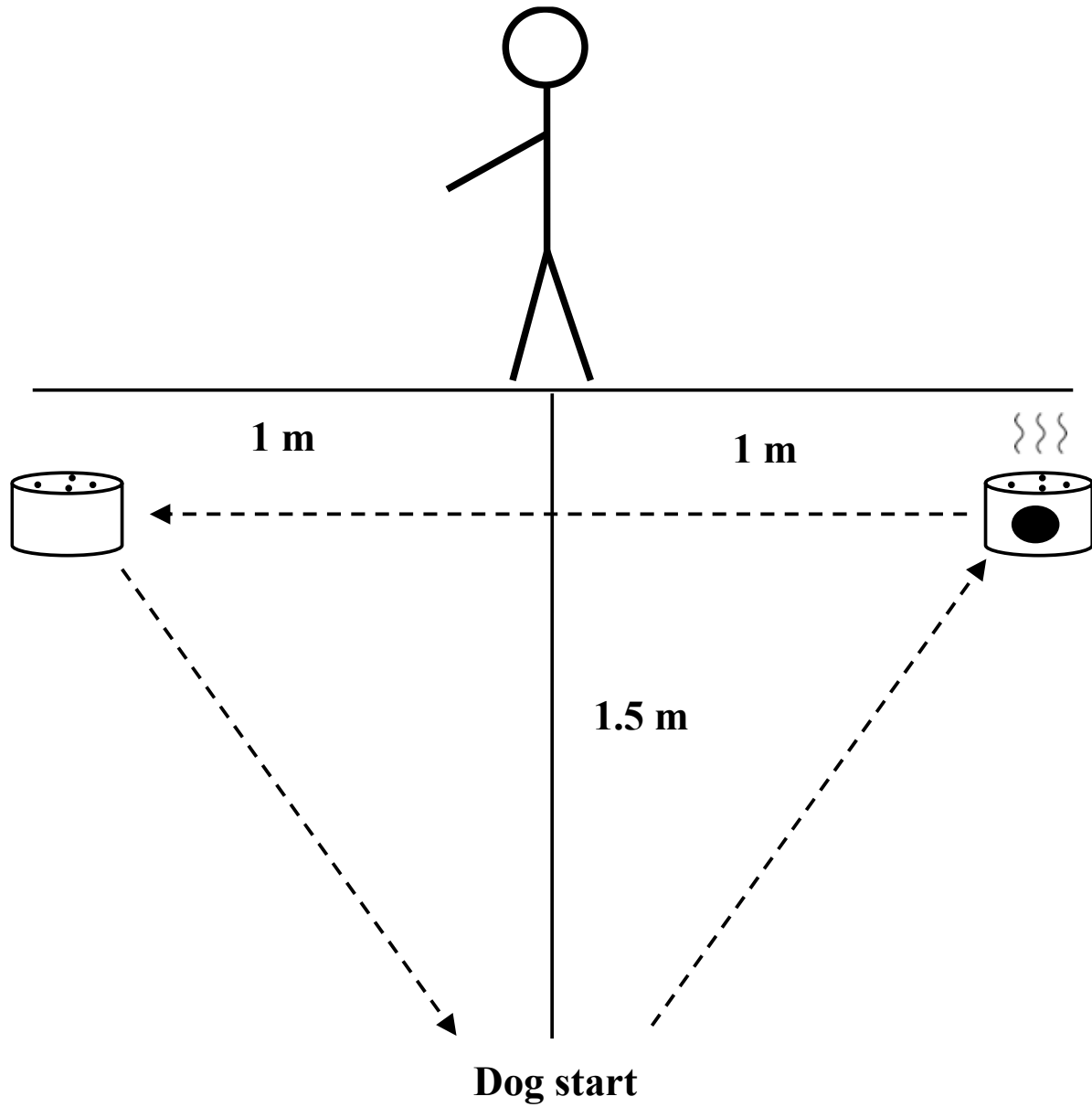


Figure 3-1. Schematic depiction of experimental setup. Dashed lines indicate dog's path.

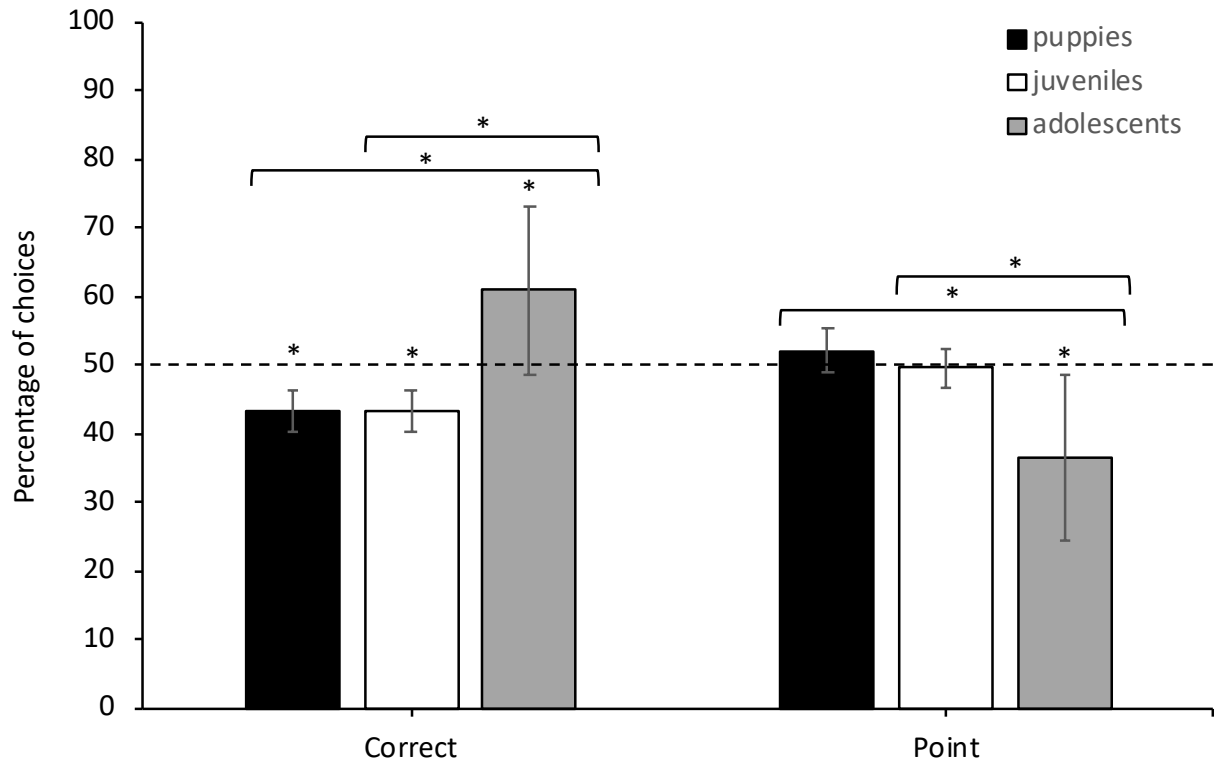


Figure 3-2. Percentage of choices to each cue as a function of age. Asterisks indicate statistically significant differences using an alpha of .05. Dashed line represents chance (50%).

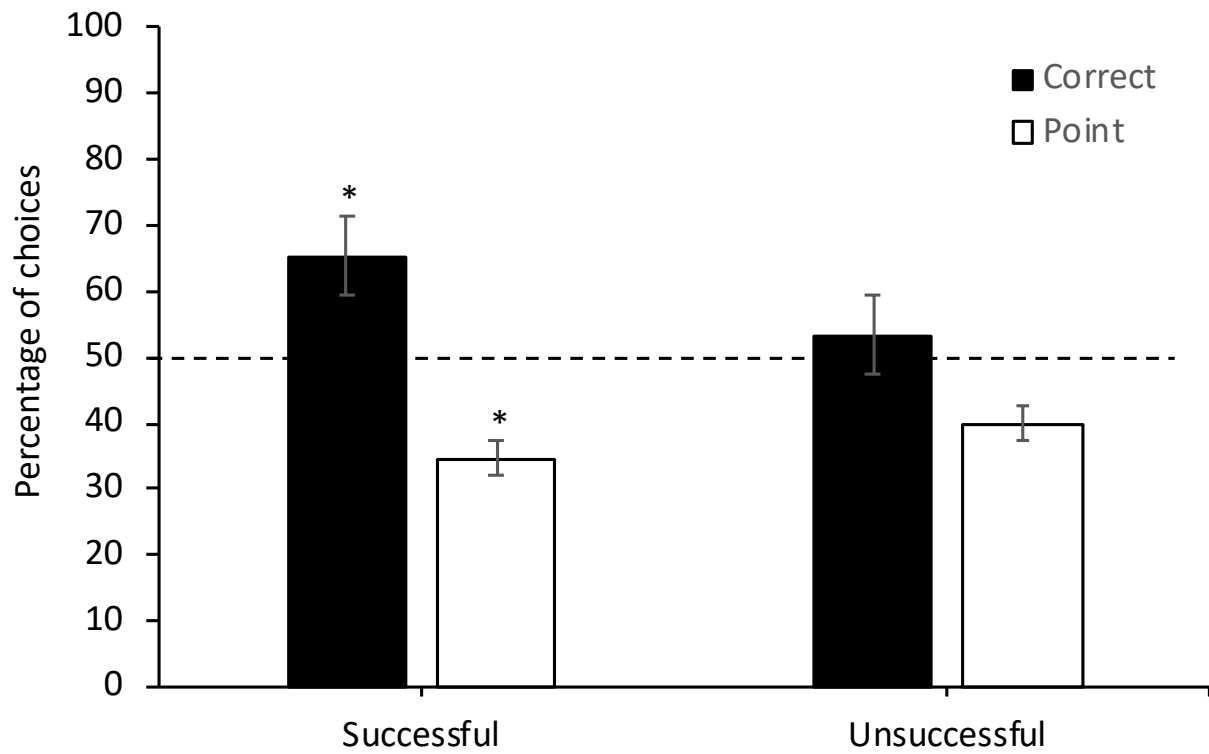


Figure 3-3. Percentage of choices to each cue as a function of outcome in adolescents. Dashed line represents chance (50%). Asterisks indicate performance statistically different from chance (alpha= .05).

Chapter IV: Development of inhibitory control in relation to detection dog success

Abstract

The study of behavioral inhibition and potential bearing on self-control has recently received increasing attention in the field of comparative psychology. Comparative developmental studies are particularly relevant to providing insights into cognitive evolution, but few studies have assessed the development of inhibitory control in non-humans. Given that inhibitory control is predictive of life outcomes, it may also have implications for the selection of successful working dogs. We tested three groups of candidate detector dogs ranging in age from 3 to 11 months on two measures of inhibitory control. We found that inhibitory control increased with age, and was predictive of future performance. However, relationships between inhibitory control and detector dog success was not straight forward and may depend on other factors such as motivation. These results extend our understanding of the development of inhibitory control to dogs, and may have important applications to working dog selection and training.

Introduction

Behavioral inhibition (also referred to as inhibitory control) is said to be exhibited when an individual suppresses a prepotent response, such as one that has been previously reinforced or appears immediately rewarding but is now ineffective, in favor of behavior that results in a successful, but sometimes delayed, outcome (Beran, 2015; Bray et al., 2014). Thus, behavioral inhibition involves self-regulation and behavioral flexibility and is critical to the ability to quickly adapt to environmental changes consisting of shifts in response-reward contingencies (Beran, 2015; Bray et al., 2014; Marshall-Pescini et al., 2015; Wallis et al., 2014). Further, behavioral inhibition is considered a component of executive function, is related to brain

capacity, and may be indicative of more complex mechanisms such as self-control (Beran, 2015; Kabadayi, Krasheninnikova, et al., 2017) Given reported associations between self-control and positive life outcomes in humans, such as academic achievement and general intelligence, the comparative study of “self-control” and other aspects of behavioral inhibition have gained significant interest (Beran, 2015; MacLean et al., 2014).

From an evolutionary perspective, behavioral inhibition is likely an adaptive mechanism important for environments with complex social and foraging dynamics (Maclean et al., 2014). For example, prey-stalking requires predators to refrain from immediately pouncing and instead waiting for the optimal moment (Bray et al., 2014). Similarly, cooperative hunting requires group synchronization, in which individuals must know when to withhold versus when to join in, which may be especially difficult in situations of high arousal (Marshall-Pescini et al., 2015). In species with complex social structures, subordinate individuals must demonstrate behavioral inhibition by deferring high value resources (e.g., mates and food) to higher-ranking individuals (Amici et al., 2018; Maclean et al., 2014). Indeed, behavioral inhibition has been shown to be associated with fission-fusion dynamics in several primate species (Amici et al., 2018).

Selective pressures may also explain inhibitory control abilities of the modern domestic dog. According to Marshall-Pescini et al. (2015), the intraspecific socio-behavioral ecologies of canid species that participate in cooperate behaviors (e.g., group hunting or communal pup raising) may have resulted in greater levels of inhibitory control compared to those that do not. Changes during domestication such as selection for tamer temperaments may also have affected inhibitory control abilities in canids. A direct comparison between wolves and identically raised free-ranging dogs revealed mixed results, and so the relative roles of ecological demands and evolutionary histories on inhibitory control remain unclear. Regardless of the reasons for these

discrepancies, the ability to exert behavioral inhibition is undoubtedly important for species living in anthropocentric environments, such as domestic dogs. For example, dogs' success in integrating into a human home involves learning to control natural behaviors such as chewing and digging, elimination, and bite inhibition. Indeed, impulsivity is considered to underlie a range of behavioral problems in dogs and has been shown to be associated with aggression, excitability, intolerance of close contact, and neophobia (Wright et al., 2011). Thus, these specific environmental demands that are unique to domestic dogs may have facilitated the species' assimilation into human societies.

In non-humans, behavioral inhibition is experimentally assessed by measuring motoric self-regulation, in which subjects must suppress some prepotent motor response. Detour paradigms, which require circumventing a transparent obstacle in order to reach a visible goal, are based on studies with human children and have been adapted for use with a diversity of species (Diamond & Goldman-Rakic, 1989; Kabadayi et al., 2018; Maclean et al., 2014). Commonly used detour tasks involve locomotor detours which require subjects to navigate around a barrier to reach a goal on the opposite side, or the so-called 'cylinder task' in which subjects must reach inside a transparent cylinder through a side opening to retrieve a reward. The tasks are considered to require inhibitory control because subjects must perform a behavioral action that is indirect, suppressing the prepotent response. For example, some versions of the locomotor detour task position the barrier (e.g., a fence) in an inverted 'V' shape such that subjects must first move away from the goal directly in front of them in order to navigate to it. In the cylinder task, the attractiveness of the clearly visible reward inside the cylinder evokes the temptation to reach for it directly which subjects must suppress by instead reaching around the side (Bray et al., 2014; Vlamings et al., 2010). Several test trials are conducted so that tactile

feedback is available given the possibility that the impermeability of the transparent barrier is not initially perceived (Bray et al., 2014). Doing so also allows for measuring the number of perseverative errors committed before successfully detouring.

Bray et al. (2015) found that arousal affected inhibitory control performance in dogs in ways consistent with the Yerkes-Dodson law in humans, which predicts a U-shaped relationship between level of arousal and performance on difficult tasks. Pet dogs and assistance dogs were tested on an inhibitory control task, with level of arousal manipulated by the experimenter exciting the dog. Compared to assistance dogs which are bred and trained to exhibit low levels of arousal, pet dogs exhibited higher levels of baseline arousal prior to the manipulation. When arousal was then increased, pet dogs' performance on the inhibitory control task decreased while assistance dogs' performance increased. The authors concluded that selection for certain temperamental profiles may shape cognitive abilities, but the effects of training were not controlled for and so it is also possible that assistance dog training increases inhibitory control. Indeed, training has been shown to enhance problem-solving abilities in dogs (Marshall-Pescini et al., 2008). Given evidence that self-control can be improved through training and practice in humans (Bray et al., 2014), it is reasonable to presume that the rigorous training undergone by assistance dogs, such as ignoring environmental distractions, could have an overall enhancing effect on behavioral regulation.

Other ontogenetic factors aside from explicit training may lead to individual variation in performance on inhibitory control tasks. Fagnani et al. (2016) compared the performance of pet and shelter dogs on two different tasks of inhibitory control in order to determine effects of past experience and life histories. The prediction was that pet dogs, living in close contact with humans, inadvertently learn to exhibit inhibitory control through interactions with owners such

as waiting to be fed, obeying commands, suppressing inappropriate behaviors, and other ways in which they adapt to living in human households. Indeed, pets outperformed shelter dogs on one of the assessments, leading the authors to conclude that environmental history, including social interactions with people, may shape inhibitory control abilities. However, a study comparing pet and free-ranging dogs failed to find differences in inhibitory control performance despite vastly contrasting life histories (Marshall-Pescini et al., 2015). Given that problems with behavioral inhibition often result in behavioral issues (Wright et al., 2011), it can also be speculated that behavioral problems with inhibitory control led to the shelter dogs' relinquishment to shelters due to their unsuitability as pets, rather than a result of the shelter environment.

Age is another developmental factor related to inhibitory control abilities. Several studies have found age-related declines in inhibitory control performance in older dogs, which corresponds with findings that the prefrontal cortex, a brain region involved in inhibitory control, declines in function with age (Bray et al., 2014; Mongillo et al., 2013; Tapp et al., 2003). This pattern is also seen in humans, which show a parabolic function of age-related increases early in development followed by gradual deterioration in older age (Williams, et al., 1999). However, aside from rhesus monkeys (Diamond, 1990) and ravens (Kabadayi et al., 2017a), the early developmental trajectory of inhibitory control has not been examined in any other species (Kabadayi et al., 2018). Doing so in dogs would be particularly valuable for providing further insights into the evolutionary and ontogenetic effects on the development of inhibitory control.

As mentioned, the study of inhibitory control has relevance to working dog populations as well as pets. Scent detection training in particular is likely to recruit inhibitory control abilities due to the high levels of self-regulation that a detection dog must employ in order to be successful. Detection dog training involves creating strong positive associations between target

odors and highly valued rewards (e.g., toys or food) using both operant and classical conditioning in order to eventually produce an automatic conditioned emotional response and trained behavioral alert to the odor. In explosives detection, dogs are trained to perform some behavioral indication in the presence of the odor such as sitting at a safe distance from the target. This response is critically important to avoid the dog coming into physical contact with the explosives which could be dangerous. However, this response can be thought to be in opposition to a dogs' natural reaction to a desirable object which would likely include excitement in anticipation of a reward, at a minimum, and possibly a predatory response towards the target (often referred to as an "aggressive response", in contrast to a "passive response"). Therefore, when detection dogs smell a target that has a strong history of conditioning, they must inhibit the prepotent response evoked by the positive association in favor of the appropriate behavioral response. Similarly, dogs must also inhibit the temptation to respond for the chance of reinforcement in the absence of trained target odors (i.e., a false indication). In addition to the scent detection aspect, other tasks performed by detection dogs also require inhibitory control such as obeying handler commands and ignoring distracting stimuli in the environment (Bray et al., 2015). These situations are especially relevant for detection and assistance dogs that often work in high-traffic, highly distracting environments with many potentially competing sources of reinforcement (e.g., a squirrel or food on the ground). Therefore, we might expect that working dog training enhances inhibitory control, and that individual level of performance on inhibitory control tasks could serve as a valuable predictor of success. Many aspects of successful detection dog performance are likely to rely on inhibitory control, but its relationship to performance has yet to be investigated (Lit, 2009).

Alternatively, it may be that highly motivated dogs perform poorly on experimental measures of inhibitory control due to a stronger desire for the reward, and that a decreased motivation to obtain the reward, an undesirable trait in detection dogs (Rooney et al., 2004), actually facilitates performance on this task. That is, in line with findings by Bray et al. (2015) that arousal interacted with performance on an inhibitory control task, dogs that are more motivated by the reward may be more greatly affected by the arousal triggered by its presence. Along these lines, Vlamings et al. (2010) found that orangutans exhibited a greater degree of inhibitory control than other species of great apes as well as human children, and suggested that this was due to the fact that they are not as enticed by the food reward as the other species that face stronger competition with group mates. Thus, individual dogs may differ in their degree of motivation for the reward which may influence inhibitory control abilities and therefore influence working performance. However, the precise relationship between inhibitory control and detection dog performance is unclear. Motivational drives, though difficult to quantify, are considered critical in the selection of suitable dogs for working roles (Beebe et al., 2016; Brownell & Marsolais, 2002; Jamieson et al., 2017). Determining these associations, as well as changes in inhibitory control over the course of development and training, may help elucidate these mechanisms and potentially provide a more objective metric of ambiguous motivational traits for selection purposes. Behavioral problems are the primary reason for rejection from working dog programs (Fadel et al., 2016), but methods to identify accurate behavioral predictors are currently lacking. The majority of research into identification of working dog traits has relied on measures of temperament, which presents challenges due to subjectivity and unreliability in measurement. Exploring cognitive mechanisms in relation to working dog ability could have important implications for the working dog industry (Lit, 2009).

The goals of this study were to assess the developmental progression of inhibitory control in detection dogs, and its relevance to detection dog performance. As few studies have examined the early development of inhibitory control in non-humans, and none in dogs, these findings can provide further insights into the cognitive evolution and ontogenetic development of inhibitory control (Kabadayi et al., 2018). Dogs are a particularly valuable point of comparison due to their unique evolutionary and ontogenetic histories with respect to domestication and experience with humans. Working dog populations offer a prime opportunity for developmental studies due to highly controlled genetic and environmental histories. Further, working dog performance outcomes can be easily tracked allowing for examination of the associations between inhibitory control and detection dog performance, which will be important for exploring parallels to the link between inhibitory control and life outcomes as in humans. Subsequently, these findings could lead to improvements in detection dog selection and training.

Recent studies comparing different tests of inhibitory control have found inconsistencies in individual performance across tasks (Bray et al., 2014; Brucks et al., 2017; Fagnani et al., 2016; Marshall-Pescini et al., 2015; van Horik et al., 2018). Thus, it has been proposed that inhibitory control represents multiple, distinct processes related to different aspects of inhibitory control rather than one unified mechanism and, accordingly, cannot be measured by one single test. Therefore, we chose to test dogs on two different tests of inhibitory control. Both tests are considered detour tasks, in which subjects must bypass an obstacle to reach a visible goal. The first task employed a reversal design, where subjects first had to learn an indirect path to a goal which was then reversed so that the opposite path was then correct. Reversal learning is considered a measure of behavioral flexibility involving inhibitory control because subjects must inhibit previously rewarded responses and shift to a new response. The second was the cylinder

task, in which subjects had to inhibit the prepotent response of reaching directly for a visible reward and instead detouring around a transparent barrier. Using two different tasks that purportedly measure the same construct, but present different task demands and possibly recruit different mechanisms of cognitive and behavioral inhibition, was advantageous for several reasons. First, it allowed for a more robust assessment of inhibitory control processes given recent uncertainties about the validity of the various measures used. Accordingly, we were then able to directly compare two dissimilar measures of inhibitory control that have not been assessed in the same population to further our understanding of the convergence of various measures of inhibition.

Methods

Subjects

We tested 78 Labrador retrievers (n=48) and Labrador retriever crosses (n=30) from a purpose-bred detection dog population on both tasks (see Lazarowski et al., 2018 for details on breeding and rearing of this population). Dogs were reared and housed under identical conditions and were part of the same development and training program from birth until approximately 12 months of age. Over the course of the training program, dogs participated in routine evaluations conducted by staff trainers designed to assess progress and performance on detection dog behavioral characteristics. For the purposes of our study and comparisons to detection dog performance, we accordingly grouped dogs into three age groups corresponding to the ages in which these evaluations occurred: puppies (N=25; mean age: 14.23 ± 1.89 weeks, 13F/12M), juveniles (N=29; mean age: 24.48 ± 1.47 weeks, 16F/13M), and adolescents, (N=24; mean age: 49.21 ± 2.4 years, 13F/11M). All dogs in our sample remained intact until matriculating from the training program, except for two males and three females in the adolescent group which were

desexed prior to testing. The majority of the dogs (n=75) participated in other assessments over the course of 2-3 days which included the two tasks in this study as well as tests of social and physical cognition and motor behavior, which are reported as separate experiments elsewhere.

Upon completion of the training program at approximately 12 months of age, dogs were presented for detection dog service to third-party customers. This process consisted of presenting dogs to target detection dog agencies who conducted independent evaluations and determined the dogs' suitability for service. Thus, for the purpose of our analyses, we categorized dogs as 'suitable' (i.e., successfully sold to a customer for detection service) or 'unsuitable' (i.e., not accepted for service as a detection dog).

General procedures

Dogs were tested in a room adjacent to their home kennel. Testing order of the tasks reported here as well as the other assessments were administered in random order. All dogs were tested on one task at a time and were returned to their home kennel for a break of approximately 30 min in between tasks. Two people participated in administering the tasks. The experimenter set up the trials, presented stimuli, and recorded trial information. The handler controlled the dog before, during, and after each trial and session. Age appropriate toys identical to those used in the dogs' daily detection training were used as rewards in the tasks. Small or medium Kong® Wubba or Squeezz Jel (depending on the dogs' size) were used for puppies and juveniles, and a Chuck It!® Ultra ball was used for adolescents. All procedures were approved by the Auburn University Animal Care and Use Committee.

Cylinder task

The cylinder task was based on the methods used by Marshall-Pescini et al. (2015) and Bray et al. (2014). A plastic cylinder (25-cm long x 25-cm diameter) was placed horizontally and

attached to a wooden board. A cloth opaque cover could be inserted and removed to make the cylinder opaque or transparent. The cylinder was placed 1 m in front of the dog and handler. On all trials, the experimenter showed the dog the toy and placed it in the center of the inside of the cylinder through the opening on the dog's right. The dog was then released and allowed 15 seconds to retrieve the reward. A correct trial was defined as retrieving the reward through the side opening of the cylinder without touching the exterior. On acquisition trials, the covering was inserted so that the cylinder was opaque and the reward was not visible after it was placed in the cylinder. Dogs were required to make four correct responses out of five consecutive trials, with a maximum allotment of 25 attempts, to proceed from acquisition to testing. Test trials were identical to training trials except that the cover was removed so that the cylinder was transparent and the reward was clearly visible inside. A total of ten test trials were conducted. Dependent measures consisted of total number of acquisition trials required to meet criterion to advance to testing, and total number of correct test trials.

Detour reversal task

The detour reversal task employed the methods of Osthaus et al (2010). A wire fence was stretched lengthwise across the testing room, pushed flush against the wall on one end leaving a gap on the other end. The fence measured 90-cm tall and approximately 5-m long when fully stretched. To account for differences in body size and speed, the length of the fence and corresponding distance from the dogs' start position to the opening was adjusted for puppies such that length of the fence was approximately 3.6-m. A 1-m wide section at the center of the fence was marked with tape on the floor to indicate the dogs' start position and for scoring purposes. Thus, the side of the fence in which the dog started each trial consisted of three

sections: the start position (inside the demarcated 1-m section), and the two sections to either side of the start area.

On each trial, the handler stood with the dog in the start area behind the fence. The experimenter stood at the center on the other side of the fence, facing the dog, and showed the dog the toy while calling the dog's name. The dog was released and allowed 2 min to cross through the opening, at which point it was rewarded with the toy and social praise from the experimenter. This sequence was repeated four times (acquisition phase), after which the fence was shifted so that the opening was now on the opposite end for four more trials (reversal phase). The order of the side of the gap was counterbalanced across subjects. The dependent measures recorded on each trial were accuracy, determined by which section of the test area the dog stepped into with its front paws first (crossing the tape and stepping into the section corresponding to the gap opening was considered correct, and crossing the line between the start position and the side corresponding to the blocked side was considered incorrect), and time to cross through the opening, defined as the time from when the dog was released until the moment the dog's head crossed the edge of the fence.

Data analysis

Developmental effects. Performance on the cylinder task was compared between age groups using a Kruskal-Wallis one-way ANOVA due to non-normally distributed data indicated by a Shapiro-Wilk test. Post-hoc analyses were performed using the Mann-Whitney U test. For the detour reversal task, a repeated-measures ANOVA with post hoc comparisons was used to assess overall age and trial effects and age x trial interactions. Independent samples t-tests were then conducted to determine specific age differences for each trial.

Relationships to working dog performance. We ran a Principal Component Analysis (PCA) on the 14-item behavioral evaluations conducted by trainers on this population as a data reduction method, which found two principal components of Performance (detection-related behaviors) and Environmental soundness (see Appendix for descriptions of each item). These two components and an overall Trainability score were correlated to the dependent measures of the tasks in the current study using a Spearman's correlation. Additionally, we compared performance on the cylinder and detour task at each age between dogs categorized as suitable or unsuitable according to their final training program outcome.

Correlations between tasks. To determine whether the same mechanisms are involved in the detour reversal task and the cylinder task, we correlated measures from both tasks using a Spearman's correlation. Previous studies have suggested that persistence is an underlying mechanism affecting inhibitory control in humans and other species (Brucks et al., 2017; van Horik et al., 2018). Therefore, because dogs in this study also participated in a task measuring persistence, we also correlated measures from that task and the current study using a Spearman's correlation.

Previous experience. Thirty-two dogs in our sample had been tested on a task involving a transparent barrier prior to the cylinder task in the current study. Because of indications that previous experience with transparent barriers could improve performance on the cylinder task, we compared the performance of the 32 dogs with prior experience to dogs without prior experience (n=43) using a Mann-Whitney *U* test.

For both tasks, each dependent measure was scored by an independent observer from video, and 20% of the sessions were double-scored by a second independent observer. Interrater reliability was excellent for the cylinder task warmup ($\kappa = .783$) and test trials ($\kappa = .915$),

and for the detour reversal task accuracy ($\kappa = .946$) and time to cross (intra-class correlation = .999).

Data for one dog (puppy group) in the cylinder task and three dogs (puppy group) in the detour task was not included due to testing error. Additionally, one dog in the juvenile group managed to squeeze through between the barrier and the wall on the blocked side during the first reversal trial. Therefore, because this dog effectively received an extra acquisition trial, only data from her first four trials were included in analyses. Due to intermittent camera malfunction during a session for one dog in the adolescent group, only data for some trials was able to be included. Finally, following Brucks et al. (2017), dogs that failed to learn the route in the acquisition phase (defined here as no correct responses in any of the four acquisition trials) were not included in the reversal. This criterion was necessary because dogs that incorrectly responded on all acquisition trials (i.e., went to the blocked side each time) likely exhibited a side bias, and reversing the contingencies would not effectively measure reversal learning if the original discrimination was never acquired (thus leading to artificially correct responses in the reversal). Two dogs in the puppy group were medically disqualified before the completion of training and therefore did not receive a categorization based on final outcome.

Results

Developmental effects

Cylinder task. Figure 4-1 shows results from the cylinder task which revealed a significant effect of age for acquisition (panel a), $\chi^2(2) = 7.219, p = 0.027$, with puppies requiring significantly more learning trials to meet criterion than juveniles, $U = 14.894, p = .045$. A significant effect of age was also found for test trial accuracy (panel b), $\chi^2(2) = 7.747, p = .021$, where puppies performed significantly worse than juveniles ($U = -15.149, p = .038$).

Detour reversal task. Figure 4-2 shows performance in the detour reversal task for the three age groups. Time to cross the barrier is represented as lines and percent correct as bars. A two-way repeated-measures ANOVA with trial (A1, A2, A3, A4) as the within-subjects variable and age (puppies, juveniles, adolescents) as the between-subjects variable was conducted on time to cross the barrier for the acquisition phase (A trials). The ANOVA revealed a significant main effect of trial, $F(1.718, 120.292) = 5.238, p = .009$, no main effect of age, $F(1,70) = 1.508, p = .229$, and no Age x Trial interaction $F(3.437, 120.292) = 1.207, p = .311$. The trial effect was due to a decrease in time from 11.285 s on trial A1, to 7.353 (A2), 5.856 (A3), and 5.263 (A4), as confirmed by a trend analyses revealing only a significant linear component, $F(1,70) = 7.183, p = .009$.

The same ANOVA conducted on percent correct for acquisition trials found no effect of trial, $F(2.895, 205.574) = 1.186, p = .316$, age, $F(2, 71) = .904, p = .410$, or Trial x Age interaction, $F(6, 205.573) = .654, p = .687$. Overall, puppies performed significantly above chance (i.e., turned towards the opening) on trials A1-4 (binomial test: A1, $p = .004$; A2, $p = .017$; A3, $p = .017$; A4, $p = .017$). Juveniles did not reach above-chance performance until trial A4 (binomial test: A1, $p = .265$; A2, $p = .265$; A3, $p = .061$; A4, $p = .024$). Adolescents performed significantly above chance on all but the second acquisition trial (binomial test: A1, $p = .0354$; A2, $p = .210$; A3, $p < .001$; A4, $p = .011$).

A similar ANOVA was conducted to assess reversal effects from trial A4 to B1, with trial (A4, B1) as the within-subjects variable and age as the between. The ANOVA revealed a significant main effect of trial, $F(1, 64) = 32.397, p < .001$, and age, $F(2, 64) = 3.784, p = .028$, and no Age x Trial interaction $F(2, 64) = 2.739, p = .072$. The effect of trial was due to a significant increase in time to cross from A4 to B1, $p < .001$. The effect of age was due to

significantly longer latencies in between puppies compared to juveniles ($p = .029$) and adolescents ($p = .014$). The same ANOVA was conducted for accuracy from A4 to B1 and revealed a significant main effect of trial, $F(1,63) = .103.633$, $p < .001$, no effect of age, $F(2, 63) = .713$, $p = .494$, and no Trial X Age interaction, $F(2, 63) = .023$, $p = .978$. The effect of trial was due to significantly lower accuracies in B1 compared to A4, $p < .001$.

To examine performance during the reversal trials, a two-way repeated-measures ANOVA with trial (B1, B2, B3, B4) as the within-subjects variable and age (puppies, juveniles, adolescents) as the between-subjects variable was conducted on time to cross the barrier. The ANOVA revealed a significant main effect of trial, $F(1.96, 125.442) = 16.771$, $p < .001$, age, $F(2, 64)$, $p = .021$; and no Age x Trial, $F(3.92, 125.442) = .998$, $p = .410$. The trial effect was due to a decrease in time from 31.148 s on trial B1 to 16.253 (B2), 12.443 (B3), and 9.432 (B4), as confirmed by a trend analyses revealing only a significant linear component, $F(1, 64) = 24.953$, $p < .001$. Post hoc tests revealed that overall, puppies had longer latencies than juveniles ($p = .02$) and adolescents ($p = .011$). Further analysis of each trial revealed that puppies had significantly longer latencies to cross than adolescents on trials B1, $t(29.462) = 2.261$, $p = .031$, and B3, $t(20.343) = 2.347$, $p = .029$. Latencies on other trials were not significantly different between age groups.

The same ANOVA conducted on percent correct of reversal trials found a significant main effect of trial, $F(2.724, 168.860) = 26.137$, $p < .001$; the main effect of age only approached significance, $F(2,62) = 2.509$, $p = .090$, and there was no Trial x Age interaction, $F(6,168.860) = .929$, $p = .475$. However, post hoc comparisons between juveniles and adolescents revealed that accuracy was significantly lower in the former, $p = .029$. The trial effect was due to an increase in accuracy from 12.341% correct on B1 to 33.175 (B2), 57.738 (B3), and 68.33 (B4), as confirmed

by a trend analyses revealing only a significant linear component, $F(1,62)= 77.849, p<.001$. Puppies fell below chance in accuracy on B1 and never recovered above-chance performance (binomial test: B1, $p< .001$; B2, $p= .664$; B3, $p<1.00$; B4, $p= .189$). Juveniles performed below chance on trials B1 and B2 (binomial test: B1, $p< .001$; B2, $p= .002$; B3, $p<.839$; B4, $p= .541$). Adolescents performed below chance on the first reversal trial, but reached above-chance performance by trial B3 (binomial test: B1, $p< .001$; B2, $p= .383$; B3, $p= .041$; B4, $p= .007$).

Working dog performance

Cylinder task. None of the dependent measures from the cylinder task correlated with dogs' training evaluation scores. When comparing cylinder task performance between suitable and unsuitable dogs, juveniles that would be ultimately categorized as suitable required more trials ($Med = 7$) to reach criterion in the acquisition phase than unsuitable dogs ($Med = 4$), $U= 20, p= .017$, (Fig 4-3a).

Detour reversal task. There was a weak but significant negative correlation between Trainability scores and average time to cross the barrier in the third reversal trial, $r_s(62) = -.27, p = .034$. Component scores for Performance traits also showed weak but significant negative correlations with average time to cross the barrier on the third and fourth reversal trial, $r_s(62) = -.26, p = .036$, and $r_s(63) = -.27, p= .03$, respectively.

Puppies. A two-way repeated-measures ANOVA for trial (A1, A2, A3, A4) and outcome (suitable, unsuitable) on acquisition trial time to cross revealed no significant effect of trial, outcome, or Trial x Outcome interaction in 3-mo old puppies, $F(1.568, 17.248) = .654, p = .497$, $F(1,11) = .027, p = .872$, $F(1.568, 17.248) = .860, p = .415$, respectively. For accuracy, there was a significant effect of outcome in that suitable dogs ($M = 93.75$) had higher accuracies than unsuitable dogs ($M = 50$), $F(1,11)= 10.911, p=.007$. There was no significant effect of trial

$F(2.157, 23.728) = .451, p = .657$, or trial X outcome interaction, $F(2.157, 23.728) = .451, p = .657$.

Suitable dogs were significantly above chance in accuracy on trials A1 and A2 (binomial test; A1: $p = .008$, A2: $p = .008$). Unsuitable dogs were not above chance on any of the acquisition trials.

For the reversal trials, there was no effect of trial, $F(2.681, 20.506) = 2.681, p = .091$, outcome, $F(1,10) = 2.803, p = .125$, or trial X outcome interaction, $F(2.681, 20.506) = .329, p = .728$ on time to cross; there were no overall effects of trial, $F(2.147, 21.468) = 1.728, p = .2$, outcome, $F(1,10) = .256, p = .624$, or trial X outcome interaction, $F(2.147, 21.468) = .192, p = .841$, but on trial B2 suitable dogs had significantly longer latencies, $t(10) = 1.642, p = .049$. Suitable dogs were below chance on trial B1 (binomial test: $p = .008$). Unsuitable dogs did not perform differently from chance on any of the reversal trials.

Juveniles and adolescents. The same analyses conducted for puppies, revealed no differences between suitable and unsuitable dogs in the two older age groups. Suitable adolescent dogs performed significantly above chance on trial A1 (binomial test: $p = .035$) and below chance on trial B1 (binomial test: $p = .003$).

Correlations between inhibition measures

No measures from the detour reversal task or cylinder task correlated with each other or with persistence.

Previous experience with transparent barriers

Neither accuracy (total number of correct responses on test trials) nor number of errors until the first correct choice differed between groups, $U = 577.5, p = .232$ and $U = 762, p = .421$, respectively.

Discussion

Candidate detection dogs ranging in age from 3 to 11 months were tested on two measures of inhibitory control in order to assess developmental effects as well as associations with detection dog suitability. We found developmental increases in inhibitory control performance similar to that of other species, and also found some evidence that inhibitory control relates to and predicts detection dog performance and suitability. To our knowledge, this is the first reported study of the development of inhibitory control in dogs, and the first exploration of its relevance to working dog performance.

Improvements in performance on both inhibitory control tasks across age groups in our study parallels evidence of developmental progressions in inhibitory control in human children (Diamond, 1990), rhesus monkeys (Diamond & Goldman-Rakic, 1989), and ravens (Kabadayi, Jacobs, et al., 2017). Developmental increases in inhibitory control tasks have been attributed to several factors including maturation of the prefrontal cortex, motor coordination, and motor-self regulation skills, as well as sensorimotor experience with transparent barriers (Kabadayi et al., 2018). In the cylinder task, we found an increase in overall accuracy on test trials between 3-month old and 6-month old puppies, but no difference between 6 and 11 month olds. Thus, we can speculate that mechanisms related to inhibitory control assessed by this task undergo a developmental progression sometime between 3 and 6 months of age in dogs. However, accuracy at 11 months was still only around 50%. Other studies testing dogs on the same procedure have reported accuracies of 70-90%, with many reporting ceiling effects in dogs as well as other species (Bray et al., 2014; Fagnani et al., 2016; Kabadayi et al., 2017; Marshall-Pescini et al., 2015). Dogs in these studies were all over 1 year of age, so it is possible that the adolescent group in our study was still maturing in this regard. However, studies suggest that the brains of dogs reach maturation by 9 months (Gross et al., 2010). fMRI studies have shown that

the frontal cortex is indeed involved in inhibitory control in dogs (Cook, Spivak, & Berns, 2016), and so differences between dogs in our study and older dogs in other studies suggest that other factors such as experience may refine inhibitory control abilities beyond this period of brain development. As such, given reported effects of experience with transparent barriers on performance in this task, we may predict earlier development of performance on this task in other dog populations such as pets that may have more experience with transparent barriers, such as sliding glass doors in their owners' homes (van Horik et al., 2018). Direct comparisons of the developmental trajectories of inhibitory control in dogs reared with different experiences in regard to transparent barrier properties will be important for disentangling learning from motor self-regulation development. For example, (Kabadayi et al., 2017a) compared raven chicks tested longitudinally on the cylinder task each week to control cross-sectional ravens tested at the same ages, and found that while prior experience on the task was not necessary for highly accurate performance in naive adult chicks, the repeated testing accelerated the emergence of high accuracy at an earlier age in the longitudinal chicks. Interestingly, though no dogs in our study reached perfect accuracy in the test trials, three dogs in the adolescent group responded correctly on 9/10 trials suggesting that the neural and motor capacity for self-regulation were apparently developed by this age, but only manifested in some dogs. These results support the suggestion that individual rather than group-level performance may be valuable in addressing the capabilities of a species or population (Kabadayi et al., 2017b).

We also found an improvement with age in the acquisition phase of the cylinder task, with 3-month old puppies requiring more trials to reach criterion with the opaque cylinder than 6-month olds. This phase of the task is not designed to measure inhibition because the barrier is opaque and thus the reward is not visible, reducing the “pull” of the visible reward which

induces direct approaches. Thus, developmental differences in this portion of the task may reflect problem-solving abilities, motor coordination, solidification of object permanence, and possibly scent-detection abilities allowing the dogs to locate the reward in the opaque cylinder.

Similar developmental patterns were found in the detour reversal task. All age groups reached above-chance accuracy levels by the end of acquisition and dropped below-chance on the first reversal trial, indicating that this task did indeed function as a reversal. However, only the oldest group recovered above-chance levels by the end of the reversal phase. Differences in latencies to cross the barrier were significantly different between age groups for the reversal trials but not the acquisition trials, indicating that developmental factors influenced reversal learning which was not confounded by differences in speed due to body size.

One explanation for why age effects only appeared on this reversal trial and not others is that age may differentially interact with the task demands which differ across trials. That is, during the first reversal trial, all dogs were equally affected by the reversal which is to be expected due to not yet having experienced the new contingencies, and reversal effects may have carried over to the second trial. By the third trial, the emergence of age differences suggests that maturation of self-regulation skills allowed older dogs to resolve the conflict more efficiently while younger dogs perseverated longer on the original route. Therefore, we can surmise that by 11 months dogs have developed abilities related to behavioral flexibility and are able to more rapidly adapt to changing contexts. As mentioned, it remains to be explored whether these results are unique to detection dogs, and whether differences are due to genetic selection for particular traits or training. It is possible that intensive training involving problem-solving, spatial navigation, and general obedience enhances cognitive flexibility and behavioral inhibition allowing for earlier emergence of these skills compared to dogs without training. Future studies

should further explore whether type and amount of training influences performance on inhibitory control tasks, as has been shown for socio-cognitive measures (Cunningham & Ramos, 2014; Marshall-Pescini et al., 2009; Scandurra et al., 2016).

As mentioned, previous experience with transparent barriers, whether due to explicit repeat testing on the same or similar tasks (Kabadayi, Jacobs, et al., 2017; van Horik et al., 2018) or incidental exposure, can influence performance on detour tasks such as the cylinder task. That is, initial errors in the testing phase when the barrier becomes transparent may be due to inexperience with the impenetrable properties of see-through objects, something not commonly encountered in natural environments, and not because of a lack of self-control (Kabadayi et al., 2018). Therefore, studies using populations of dogs such as pets or shelter dogs, in which previous experience or life history is unknown or cannot be controlled for, should be interpreted with caution. In our study, dogs were born, reared, and housed in identical conditions and experienced the same training procedures. Therefore, while specific experience with clear surfaces was not controlled for or taken into account in interpreting our results, dogs in our sample should not have differed from each other in this regard. Many dogs in our population were however tested on a separate task that involved transparent objects. To determine whether this could have influenced performance in the current study, we compared performance between dogs that had participated in that task to dogs that had not, and did not find that this experience influence performance. While it is known that previous experiences with relevant stimuli influence detour task performance, this particular experience was likely too brief to have an effect. Nonetheless, the ecological validity of transparent barrier tasks should be taken into account. Kabadayi et al. (2018) recently recommended that subjects tested on inhibition tasks

have adequate experience with transparent surfaces to learn about their physical properties before testing.

We also found some associations between performance on inhibitory control tasks and detection dog success, which varied by age. For the cylinder task, juveniles that would ultimately be successfully placed in service were characterized by requiring more trials to meet criterion with the opaque cylinder than dogs that would fail to be placed in service. For the detour reversal task, several trainer-rated scores of detector dog behaviors correlated with test performance including inverse relationships between reversal trial time to cross and Trainability as well as Performance scores, and a positive relationship between average time to cross during acquisition and Environmental soundness. Regarding program outcome, puppies ultimately categorized as suitable had higher overall accuracies in the detour task acquisition phase than those not suitable and performed successfully above chance on more trials than unsuitable dogs, but had longer latencies to cross the barrier in the second reversal trial.

These results are somewhat in line with findings that problem-solving speed and perseveration were predictive of assistance dog outcomes (Bray et al., 2017), and partially supported our predictions that inhibitory control would play a role in detection dog performance. Although no correlations were found between trainer-rated scores of detector dog behaviors and cylinder task performance, correlations with detour reversal performance, though small, hint at the existence of underlying mechanisms of behavioral inhibition in detector dog performance. For example, it is not surprising that dogs scoring low on Trainability, the trainer-rated measure of the speed and efficiency in which a dog learns new tasks, tended to take longer to cross the barrier during the third reversal trial. Thus, dogs' ability to adapt to the reversed detour after several repetitions likely reflects overall learning ability (i.e., trainability). Similar inverse

relationships between time to cross during reversal trials and Performance scores indicates that motivational factors may underlie performance on the detour reversal task. Performance ratings were composite scores of several detection-related behaviors including dogs' ability to search and hunt, as well as overall focus and desire for the rewards, and independence. Thus, greater overall motivation for obtaining the reward may have facilitated more rapid learning during the reversal. This explanation may also account for the other relationships found. Higher overall accuracies in the acquisition phase of the detour reversal task in ultimately successful puppies compared to those not successful may again reflect motivational variables that drove performance. However, these same puppies also had longer latencies on the first reversal trial, which is seemingly contradictory to this interpretation. One explanation is that high motivation to obtain the reward results in elevated states of arousal, which is exacerbated when the detour is first reversed and presents a significant challenge. This arousal may then interfere with the ability to problem-solve. Thus, level of arousal in highly motivated versus less motivated dogs may account for this counterintuitive result. This interpretation is in line with findings by Bray et al. (2015) that arousal interacted with dogs' baseline arousal level to either enhance or interfere with performance. The assistance dogs tested in the study, which have been bred and trained to exhibit calm and non-excitability temperaments, contrast with detection dogs such as those in our population which have experienced selection for traits leading to high-energy and arousal, including impulsivity (Fadel et al., 2016). Therefore, performance in this task may effectively distinguish between a phenotypically ideal detection dog with those that lack the necessary motivation and accompanying arousal, or are better suited for other working roles. Further, differences in detour reversal performance between suitable and unsuitable dogs were apparent in puppies as young as 3 months, suggesting that performance on inhibitory control tasks may be

a valuable predictor of future performance. Future studies directly comparing inhibitory control between populations of dogs bred and trained for different working roles early in development may reveal worthwhile differences in underlying mechanisms of inhibition that may be useful in selection and training of dogs for these roles.

The lack of consistency in performance on the two detour tasks used in our study adds to increasing evidence that different tasks purported to measure inhibitory control do not correlate with each other (Bray et al., 2014; Brucks et al., 2017; Fagnani et al., 2016; van Horik et al., 2018). These inconsistencies have led to questioning the construct validity of commonly used inhibitory control tasks, and suggestions that inhibitory control is a multi-faceted, domain- and context-specific process (Bray et al., 2014; Brucks et al., 2017; van Horik et al., 2018). Indeed, van Horik (2018) found that pheasants' individual performance on two different measures of inhibitory control was inconsistent and instead related to other factors such as previous experience with transparent barriers and persistence measured by number of pecks to an inaccessible reward. Because the majority of dogs in our study also participated in a separate study that measured persistence, we were able to test for this relationship and did not find an association between persistence (measured by attempts to access an inaccessible reward) and inhibitory control. The fact that relationships between task performance and detection dog success showed different patterns further demonstrates the discrepancies between the two measures, and may suggest that they are measuring different processes.

As discussed, motivational factors, including type of reward used and individual level of motivation, as well as physiological state (e.g., arousal) can also influence test performance unrelated to the cognitive capacity to solve the task (Bray et al., 2015; Kabadayi et al., 2018; Shaw, Boogert, Clayton, & Burns, 2015). Indeed, many non-cognitive factors are thought to

influence performance on different measures of inhibitory control that may lead to discrepancies in task performance. For example, rearing conditions have been suggested to affect inhibitory control task performance (Kabadayi et al., 2018), which may explain why pets outperformed shelter dogs in one type of measure (Fagnani et al., 2016). However, this difference was only apparent in one of the two tasks used, which again highlights the specificity of inhibitory control tasks. Regardless, dogs in our population were housed under identical conditions and received ample social, physical, and mental enrichment via daily playful interaction with trainers and conspecifics, physical exercise, access to a variety of toys, and occupational enrichment provided through training activities. Thus, housing conditions are not likely to have influenced inhibitory control performance in our population.

Neophobia has also been thought to hinder an animal's ability to perform cognitive tasks due to a fear of approaching the objects or experimenters (Kabadayi et al., 2018; Shaw et al., 2015), and Wright et al. (2011) found that impulsivity was related to fear of novelty. Because behavioral problems including fearfulness are one of the greatest reasons for release from working dog programs (Evans et al., 2007), we anticipated that good performance on the cylinder task would be predictive of dogs *not* successfully placed in service. We expected bolder dogs to be less fazed by the tactile feedback from physical contact with the barrier and more fearful dogs to approach the apparatus more cautiously, avoiding the potentially aversive physical contact with the barrier. This prediction was not supported by our analyses in that no differences were found between suitable and unsuitable dogs in the cylinder task test trials. However, despite the lack of statistically significant differences, unsuitable dogs were on average more successful on test trials and made fewer errors before the first correct choice than suitable dogs. Considerably unequal sample sizes in our suitable and unsuitable groups may have

contributed to a lack of power to detect these differences. However, we did find that in juveniles, suitable dogs required more acquisition trials to meet criterion with the opaque cylinder. Because this phase of the task does not ostensibly assess inhibition as the barrier is not transparent, these differences may also have been attributed to neophobia related to touching the apparatus.

In sum, we found that the development of behavioral inhibition in puppies follows a similar increase during development to that of human and non-human primates and birds. These results may provide further insights of the phylogenetic landscape of inhibitory control across species. Given that this is the first investigation of the developmental trajectory of inhibitory control in dogs, future research is needed to further explore effects of experience, including training and environment, on cognitive development. Our findings that some aspects of inhibitory control performance were related to and predictive of detection dog success also have practical applications to selection and training for the working dog industry. Future research is needed to expand on these findings to determine the particular mechanisms that are associated with success.

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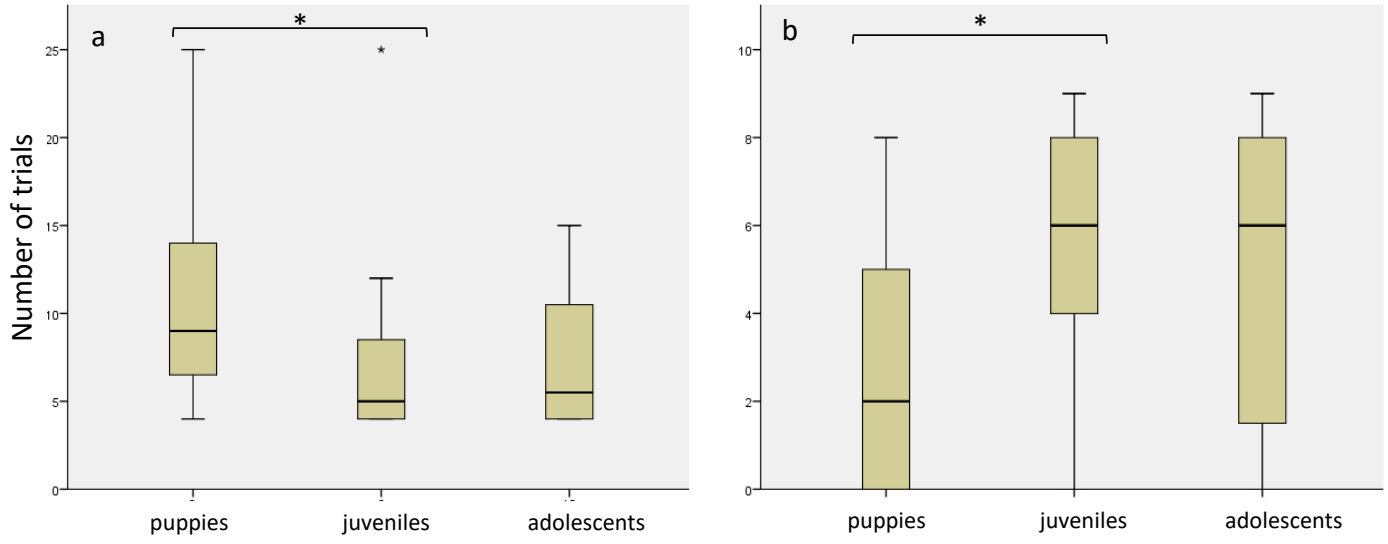


Figure 4-1. Performance on the cylinder task for acquisition trials (a) and test trials (b) as a function of age.

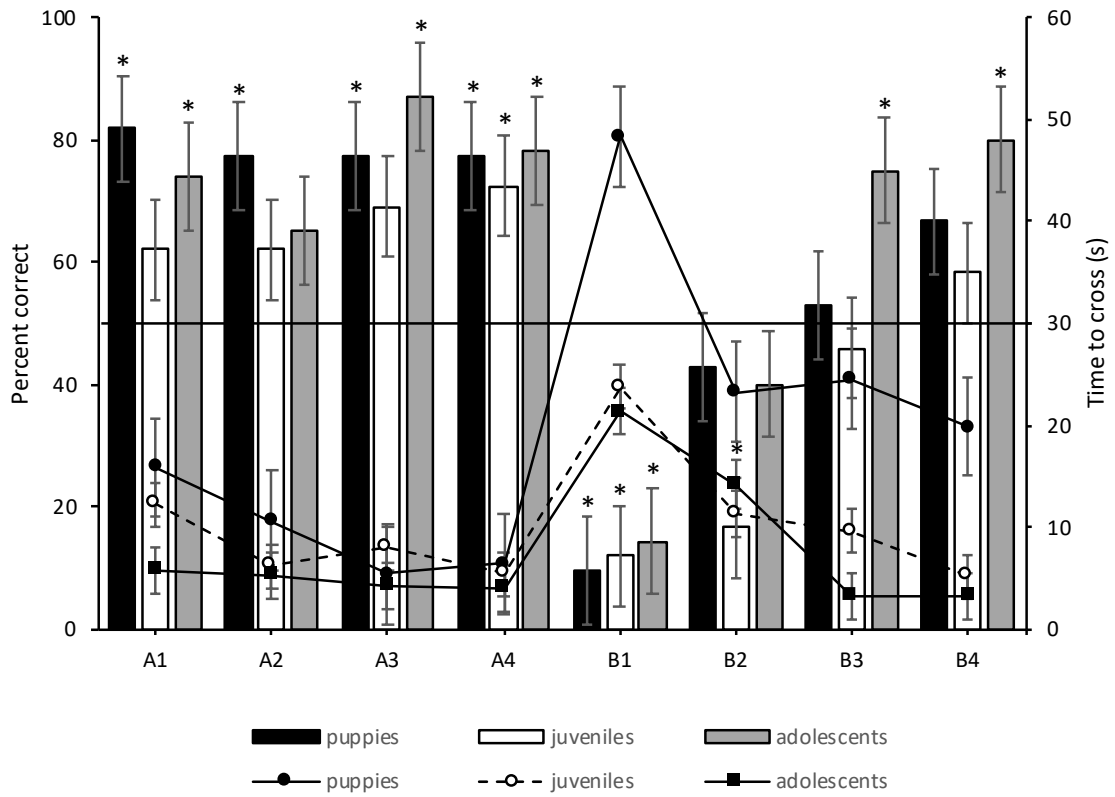


Figure 4-2. Time to cross barrier (lines) and percentage correct (bars) for each trial as a function of age for the detour reversal task. Asterisks indicate performance significantly above chance (binomial test, $p < .05$).

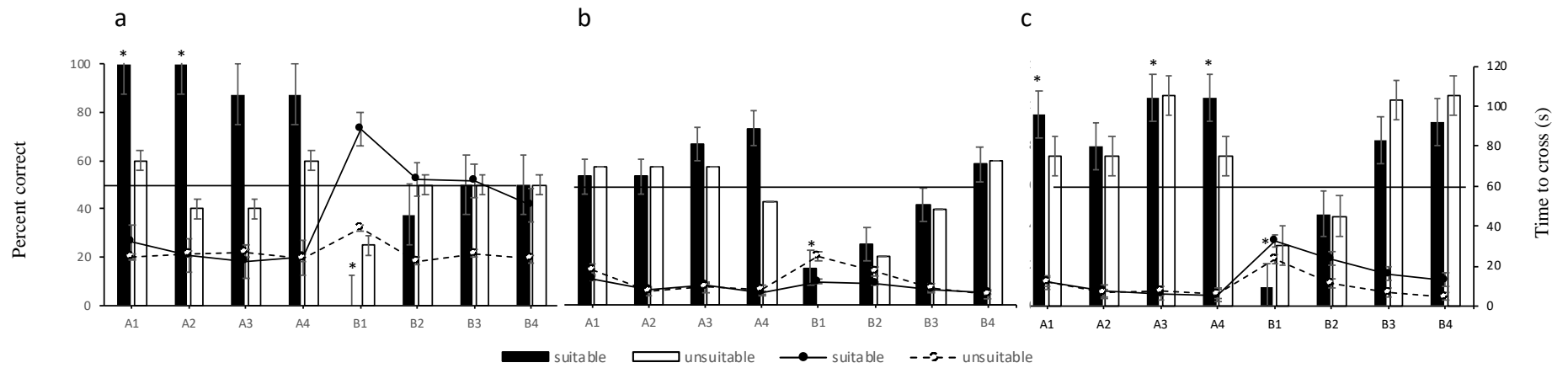


Figure 4-3. Percent correct for each trial of the detour reversal task for puppies (a), juveniles (b), and adolescents (c) as a function of program outcome (suitable, unsuitable).

Chapter V: Ontogeny of detection dogs' understanding of hidden objects

Abstract

The cognitive capabilities of dogs have been shaped by both ontogenetic and phylogenetic factors, resulting in heightened social sensitivity at the cost of reduced physical problem-solving abilities. Understanding of the physical world develops with maturation and experience in humans and other species, but little is known about how developmental experiences might facilitate learning in this domain in dogs. This study explored the nature of the development of physical problem-solving in a cohort of candidate detection dogs using three object-search tasks targeting domains related to object permanence and causal inference. We assessed the ontogenetic development of these abilities and evaluated performance on each task in relation to dogs' suitability as a detection dog. Overall, our results support conclusions that dogs' abilities to represent physical objects are limited, but show developmental trajectories similar to other species. We also found associations between successful detector dog performance and understanding of the physical properties of objects.

Introduction

Given the significance of dogs in human society it is not surprising that the social behavior of dogs has been thoroughly examined, revealing impressive abilities in the ways dogs interact with humans. Conversely, much less attention has been given to dogs' problem-solving behavior in non-social contexts. Animals' abilities to properly interact with the environment is shaped by ecological demands related to foraging, navigation, and group dynamics, and are influenced by both genetic predispositions and developmental experiences (Miklosi 2015). Whereas the social capabilities of dogs have been greatly molded by genetic selection and

behavioral conditioning for adaptation to life with humans, physical problem-solving abilities may have been stunted due to relaxed ecological pressures stemming from a buffering effect of human provision (Bräuer et al., 2006; Lampe et al., 2017). Modern domesticated dogs exist in a range of contexts in our society, from companion pets to dogs serving various functional roles such as guiding the disabled and detecting contraband. Exploring physical-ecological problem solving in populations of dogs from varying environments, with differing cognitive and behavioral demands, is necessary for furthering our understanding of their extents and limitations and the interplay between genetic history and environment (Miklosi 2015).

The ability to navigate through space and track the trajectories and locations of moving objects are critical skills for reasoning about the physical world (Miklosi 2015; Rosati, et al., 2014). Canids and other species require these abilities in order to navigate to and from hunting and home territories, locate caching sites, and catch prey (Fiset et al., 2007; Miklósi, 2015). Tracking and locating objects that are out of sight have clear adaptive value for behaviors that require maintaining mental representations of other individuals that have moved out of the field of view, such as moving prey, hunting partners, or mates (Fiset et al., 2007; Miklosi 2015).

Many non-human species are presumed to possess object permanence, or the ability to mentally represent an object that is out of sight (Miklosi, 2015). Experimentally, object permanence is assessed using visible displacement tasks in which subjects witness the hiding of an object in a concealed location. Goal-directed search for the object at the correct location is taken as evidence of the individual's ability to mentally represent the object that is no longer perceptually available. Versions of this task have also been used to assess working memory for the object's location by inserting a delay between the time the object is hidden and when the subject is released to search (Fiset et al., 2007; Gagnon & Doré, 1993; Hunter, 1913). A more

complex version of the visible displacement task, *invisible* displacement, involves placing the object inside a transport container that is then moved to a new concealed location (e.g., behind a screen) where the object is deposited; thus, the hiding of the object occurs out of view. After the transport container is returned and revealed to be empty, the location of the object must be indirectly inferred by the trajectory of the transport container. Ecologically, animals are thought to face such invisible displacement problems when tracking an object or individual that disappears behind a hiding location and continues to move while out of sight (Fiset & Plourde, 2013).

Comparative studies suggest that, besides humans, few species are able to solve more complex invisible displacements including great apes and corvids. While dogs are able to correctly locate hidden objects in invisible displacement tasks, further exploration of search behavior has revealed that dogs appear to use simple associative rules that rely on perceptual cues to locate the objects, and are unsuccessful when these factors are controlled for; thus, conclusions that dogs can mentally represent the movement of hidden objects have been challenged (Collier-Baker, 2004; Fiset & LeBlanc, 2007). Dogs also tend to be heavily influenced by human actions on such tasks, searching locations last seen touched by a human even when clearly empty (Erdohegyi et al., 2007; Miller et al., 2009). For example, like children, dogs are more likely to commit the *A-not-B* perseverative error (i.e., continuing to search in an object's original location after observing it hid in a new location) if the objects are moved by humans, but do not make the error if the social component of human involvement is removed (e.g., objects are moved by strings) (Gagnon & Doré, 1994; Topál et al., 2009; Topal et al., 2008).

Species differences in physical problem-solving abilities have led to questions about the corresponding effects of ecological context and evolutionary history. Rooijakkers et al. (2009) tested dogs and great apes on the transpositions, a form of invisible displacement in which an object is placed in one of two containers which are then manipulated by moving one or both to different locations. Dogs were successfully able to locate the object on trials in which the baited container moved to a new location and its original location remained empty. However, when the baited container moved to a new location but the original position was substituted by the other (empty) container, dogs tended to search in the original location. Further, performance was disrupted if the containers crossed paths with each other. Consistent with the hypothesis that dogs' physical cognition may be hindered due to relaxed ecological pressures for problem-solving corresponding to the development of a reliance on humans for solving problems for them, great apes outperformed dogs on all conditions and excelled at even the most difficult type of transposition in which both containers moved, crossed paths, and swapped positions. Similarly, great apes have also outperformed dogs in tasks requiring the use of indirect causal cues to locate objects, such as the noise produced by shaking a container with an object inside versus an empty container (Bräuer et al., 2006). This difference in performance between the two species was attributed to the evolution of cognitive skills for solving foraging-related problems in the physical world, such as extracting non-perceptible food items from hidden locations (e.g., inside bark) using indirect visual or auditory cues to infer their location. On the other hand, when the cues indicating the location of the hidden reward were social (e.g., a human pointing to the container) rather than physical, dogs outperformed apes. The authors argued that the process of domestication, during which dogs became increasingly reliant on humans, may have led to a trade-off between increased social and physical problem-solving abilities (Bräuer et al., 2006).

Indeed, comparisons to dogs' wild counterparts have revealed that wolves, even if socialized to humans, are not susceptible to human biasing during the *A-not-B* task as dogs and children are, further implicating how domestication may have shaped canine cognitive abilities (Topál et al., 2009). However, an alternative possibility is that dogs' reliance on humans develops due to everyday experience living under the care of humans, thus reducing the need for physical problem-solving skills (Udell et al., 2010). In order to disentangle these effects, Lampe et al. (2017) compared dogs, both human- and pack-raised, to wolves in their ability to locate rewards using social and causal cues. While all groups were able to use the social cues, only the wolves were successful in using the causal cues and no differences emerged between the two dog groups. This difference between the canid species, but not between domestic dogs differing in life experience, provides further support for the hypothesis that reduced physical problem-solving abilities are due to domestication and not differences in human experience or lifestyle. By contrast, other studies have reported no difference between dogs and wolves on tests of object permanence and invisible displacement, and point to ecological differences in canid's evolutionary history compared to that of great apes and some bird species rather than more recent changes during domestication (Fiset et al., 2014; Fiset & Plourde, 2013). That is, canines probably do not need skills for finding objects that have disappeared and moved imperceptibly using visual cues; rather, they are more likely to search for prey at the location they saw it disappear, and then use their primary sense of olfaction to continue the pursuit (Fiset & Plourde, 2013). These mixed results indicate that physical problem-solving abilities for locating hidden objects may be task- or domain-specific, requiring different skills for tracking the movement of objects versus understanding causal cues. Further investigation of these abilities in dogs differing in domestication and/or experience is needed to clarify these differences (Lampe et al., 2017). In

particular, in contrast to the assumption that evolutionary changes have led to restricted physical-problem solving abilities in dogs and/or canids in general, whether these abilities can be enhanced through selection for particularly breed-specific traits or through specialized training needs to be addressed.

Humans typically develop behaviors reflecting object tracking abilities in a consistent pattern during early development originally described by Piaget (1952), beginning with object permanence and progressing in complexity through different levels of invisible displacement. In human children, the cognitive processes enabling these skills emerge throughout ontogenetic development via playful manipulation, exploration, and interactions with an individual's social and physical environment (Gagnon & Doré, 1994; Müller et al., 2016). Comparative research has used tests of object permanence and related abilities for assessments of species' cognitive capacities, but few have investigated the ontogenetic development of these processes and even fewer in non-primate species (Gagnon & Doré, 1994). In the only reported study of the development of object permanence in domestic dogs, Gagnon & Doré (1994) found that puppies were able to succeed on visible displacement tasks by the 8th week, coinciding with the weaning period. Beyond the 8th week, no further significant development on more complex invisible displacement was observed as a group, but a few individual 11-mo olds were able to successfully solve the single invisible displacement task. More recently, this study was replicated in wolf puppies whose performance indicates similar developmental patterns to dogs (Fiset et al., 2014). Gagnon & Doré (1994) concluded that the development of object permanence in dogs differs in rate and capacity from other non-canid species, and emphasized the value of developmental studies in clarifying how cognitive structures evolve and are shaped by development and ontogenetic experiences (Gagnon & Doré, 1994). Overall, comparative research has shown that

many species are capable of at least some forms of object permanence and object tracking abilities, but indicates a lack of a uniform developmental trajectory as seen in humans (Rosati et al., 2014).

In contrast to the extensive literature on the effects of both domestication and experience on dogs' social cognition, and reports of phylogenetic effects on physical problem solving, little is known about the effects of experience in this domain. Dogs present an ideal opportunity for the study of ontogenetic effects because within the species, there are various sub-populations with diverse environmental histories. Given that the literature on dogs' physical problem-solving abilities thus far have relied on pet dog subjects, findings may not be representative of dogs as a species. That is, the unique environment of pets living in human homes may have shaped (or hindered) particular problem-solving abilities compared to dogs in other contexts, as has been shown for socio-cognitive abilities. Working dogs in particular provide a rich opportunity for the study of the development of cognitive abilities. They are typically bred from the same population and reared under controlled conditions, thus minimizing genetic (i.e., breed) and environmental differences. Further, the cognitive demands imposed by working dog training and occupational requirements may facilitate the development of more advanced cognitive function. Scent detection dogs, which are used to detect a range of chemical and biological targets (Helton, 2009), may be particularly worthy of study due to the specific nature of their training. Detection dog training involves play and exploration using a variety of objects beginning at an early age, such as retrieving toys that have been thrown out of sight. Operationally, detection dogs are constantly searching the environment for objects that are out of their perceptual field. Thus, we might predict that these experiences facilitate the development of physical problem-solving abilities at a faster rate or greater degree than dogs without these explicit experiences. Another

possibility is that if cognitive mechanisms are indeed associated with working dog performance, it may be possible to identify early cognitive markers of future success. Given that the identification of successful dogs at an early age—something that has proven to be a challenge—would greatly reduce costs and time associated with the preparation of a candidate, there are clear implications for the working dog industry.

The primary aim of the current study was to explore the ontogenetic development of cognitive abilities pertaining to physical problem-solving in a population of candidate detection dogs. Specifically, we examined varying degrees of object permanence, delayed visual search for disappearing objects, and causal reasoning. Few studies have examined dogs' abilities in these tasks, few of which have been examined developmentally or in populations with varying life experiences that may shed light on ontogenetic effects. We tested three cross-sectional age groups in order to determine developmental effects, and tracked dogs' training program outcome success in order to determine whether performance on the cognitive tasks were predictive of detection dog suitability.

Methods

Subjects

Subjects ($n = 75$) were candidate detector dogs, consisting of Labrador retrievers/Labrador retriever crosses, from the same purpose-bred detection program where they experienced the same socialization and training for detector dog work from birth through approximately 12 months. Throughout this period, at approximately 3, 6, 11, months of age, dogs were evaluated for their training progress. At the completion of training at approximately 12 months, dogs were presented for detector dog service to third-party agencies who made decisions to either accept or reject based on their independent evaluations of the dogs' detector dog

suitability. Thus, all dogs received a final outcome depending on their successful or unsuccessful placement in service as a detector dog.

We grouped dogs into three cross-sectional age groups corresponding to the ages at which dogs were evaluated: puppies (N=24; mean age: 14.23 ± 1.89 weeks, 13F/11M), juveniles (N=27; mean age: 24.34 ± 1.44 weeks, 15F/12M), and adolescents (N=24; mean age: 49.21 ± 2.4 weeks, 13F/11M). All dogs were intact except for two males and three females in the adolescent group which were desexed during the month prior to testing.

General procedures

Each task, described below, was adapted from the dog cognition test battery developed by MacLean et al. (2017). The tasks reported here were part of a broader assessment administered to dogs over the course of 2-3 days, which are reported as separate experiments elsewhere. Tests were administered in random order with breaks of approximately 30 min in between. Testing was conducted in a room adjacent to the dogs' home kennel. Two people participated in each task: the experimenter set up the trials, presented stimuli, and recorded trial information, and the handler controlled the dog before, during, and after each trial and session. All procedures were approved by the Auburn University Animal Care and Use Committee.

Delayed response task

This task measured dogs' ability to locate a visually displaced object after a delay of 0, 10, 40, or 60 s. Three large identical opaque cups were placed up-side down in a horizontal line, 1 m apart, 1.5 m in front of the dog. On each trial, the experimenter held up the toy and placed it in under one of the three cups. After a given delay, the dog was released and allowed 15 s to make a choice. A choice was defined as the dogs' head coming within 10 cm of a cup. If the baited cup was chosen, the experimenter lifted the cup and rewarded the dog with the toy. If

either of the two empty cups were chosen, the experimenter lifted it to reveal that it was empty. Twelve trials were conducted, with three trials for each delay. The 0-delay trials were conducted in the first three trials to serve as the baseline and warmup before the delayed trials began. The delay trials were then presented in random order across the remaining trials. Trials were counterbalanced so that each position (left, middle, or right) was baited three times, with no more than two trials in a row in the same location.

Transpositions

This task measured dogs' ability to track the location of a visibly displaced object through various transpositions. On each trial, two large identical opaque cups were placed upside down in a horizontal line in front of the dog in a predetermined position. The experimenter showed the dog the toy, placed it under one of the two cups in front of the dog, and then moved the cups according to the corresponding transposition. Three types of transpositions were performed (see Figure 5-1), with each type corresponding to a different level of difficulty depending on whether one or both cups moved, whether the cups moved to a new position or replaced the original position of the other cup, and whether or not they crossed paths. In all cases, the experimenter placed a hand on each cup at the same time and released both at the same time after the transposition was complete. Dogs were released to make a choice as soon as the experimenter released the cups and were allowed 15 s to respond. A correct choice was defined as touching the baited cup with the head or front paw, and an incorrect choice was defined as touching the empty cup. As soon as a choice was made, the experimenter lifted the cup to reveal its contents and allowed the dog to obtain the toy if correct. Four trials were conducted for each type of transposition, for a total of 12 trials. Trials were conducted in blocks of increasing

difficulty. Within each block, the position (left or right) of the baited cup and the direction of its movement was counterbalanced across the four trials.

Causal reasoning

This task measured dogs' ability to infer the location of a hidden reward based on auditory cues. Two large identical opaque cups with a lid were positioned approximately .5 m on either side of the experimenter, one of which was baited out of the dog's view before each trial. The dog was positioned 1.5 m in front of the experimenter and watched as the experimenter picked up and shook each cup for approximately 3 s each (always starting with the cup on the right). The location of the reward could be inferred based on the sound made from the toy rattling inside the cup when shook, compared to no sound made by the empty container. Ten trials were conducted, counterbalancing the location of the reward.

Odor control

To determine whether dogs could locate the reward using olfactory cues, 10 trials were conducted identical to the delayed response task except only two containers were used, dogs did not witness the baiting of the container, and dogs were released immediately after the container was baited. Trials were counterbalanced so that the left and right containers were each baited 5 times, no more than twice in a row.

Data analysis

For the delayed-response and transpositions task, developmental effects were assessed by a repeated-measures analysis of variance (ANOVA) with age as the between-subjects factor and trial type as the within-subjects factor. Greenhouse-Geisser corrected degrees of freedom were used for violations of assumptions of sphericity. Post hoc tests (LSD) were used to determine which age groups differed, and independent samples *t* tests were used to compare group

performance for each trial type. For the causality task, developmental effects were assessed by a one-way ANOVA comparing performance between groups. For all tasks including odor controls, a one-sample *t* test was used to compare the performance of each group against chance (33.33% for the delayed response task, 50% for transpositions, causality, and odor controls), and individual performance was compared to chance using a binomial test (performance of 7/12 was considered significantly above chance for the delayed-response task, 10/12 for transpositions, and 8/10 for the causality and odor controls). To determine whether performance on a task was predictive of program outcome, we categorized dogs according to final outcome as ‘suitable’ (successfully sold for service) or ‘unsuitable’ (not successfully sold for service). Separate one-way ANOVAs for each age group on each task were used to determine whether performance differed as a function of outcome in the program. Follow-up one-sample *t* tests were used to compare each group’s performance to chance. A Spearman’s correlation was used to correlate task performance to PCA-generated composite-scores from training evaluations (Appendix). Double-scoring of 20% of the videos yielded excellent inter-rater agreement (Delayed-response task, Cohen’s kappa= .812; transpositions task, Cohen’s kappa= .849; causality task, Cohen’s kappa=: .860).

Results

Odor controls

A subset of dogs (20%) was tested for their ability to locate the reward, hidden out of view and presented with no ostensive cues, based on scent alone. Dogs chose the baited container at chance levels, $t(12) = -1.328$, $p = .209$, and no dogs were above chance at the individual level (at least 8/10 correct, binomial test).

Developmental effects

Delayed-response. Figure 5-2 shows developmental effects in the delayed-response task. There was no effect of delay, $F(2.938, 208.591) = 1.628, p = .202$, or Delay x Age interaction, $F(5.876, 208.591) = 1.520, p = .174$. There was a main effect of age, $F(2, 71) = 20.899, p < .001$. Post hoc tests revealed that overall, adolescents performed significantly better than puppies ($p < .001$) and juveniles ($p < .001$). Further analysis of group differences at each delay revealed that adolescents outperformed puppies at each delay ($ts[45] > -2.83, ps < .008$), and outperformed juveniles at each delay ($ts[49] > -3.18, ps < .004$) except for 60 s ($t[49] = -.691, p = .493$).

Comparing each group's performance to chance (33.33%), puppies did not perform differently from chance at any of the delays ($ts[22] > -.525, ps > .383$); juveniles performed above chance at the 10-s delay, $t(26) = 2.295, p = .030$, and 60-s delay, $t(26) = 2.181, p = .038$; and adolescents performed above chance at every delay ($ts(23) > 3.45, ps < .003$). At the individual level, 3 puppies, 6 juveniles, and 17 adolescents performed significantly above chance overall (at least 7/12 correct responses, binomial test, $p = .047$). Age had a significant effect on percentage of non-response trials, $F(2, 73) = 4.843, p = .011$; post hoc tests revealed that puppies committed significantly more non-responses than juveniles ($p = .022$) and adolescents ($p = .004$).

Object transpositions. Figure 5-3 shows effects of trial type on percent correct, $F(1.701, 122.480) = 32.286, p < .001$, as well as an interaction between trial type and age, $F(3.402, 122.480) = 9.014, p < .001$, but no overall effect of age, $F(2, 72) = 1.216, p = .303$. Post hoc tests revealed that performance was significantly higher in the *no cross—both new* condition compared to the *single-cross—one new* condition ($p < .001$), and the *double-cross switch* condition ($p < .001$), but no difference between the second two conditions ($p = .222$). Comparing group performance to chance, puppies performed significantly below chance in the *double-cross switch* condition (i.e., choosing the location where the object was last seen); juveniles performed

at chance levels on all three conditions $t(23) = -2.882, p = .008$; adolescents performed above chance in the *no cross—both new* condition, $t(23) = 7.123, p < .001$, and below chance in the *single-cross—one new*, $t(23) = -2.632, p = .015$, and *double-cross switch* conditions, $t(23) = -5.791, p < .001$. Comparing performance between the age groups at each level of difficulty, adolescents performed better than puppies, $t(46) = -3.945, p < .001$, and juveniles, $t(49) = -3.763, p < .001$, in the *no cross—both new* condition. In the *double-cross switch* condition, adolescents performed worse than both puppies, $t(46) = 2.043, p = .047$, and juveniles, $t(49) = 3.455, p < .001$. At the individual level, no dogs from any of the three groups performed significantly above chance (at least 10/12 correct responses) overall. There was no effect of age on percentage of non-response trials, $F(2,74) = 1.620, p = .205$.

Causality. There was no effect of age on accuracy, $F(2, 82) = .017, p = .983$. Performance did not differ from chance for any of the ages as a group. At the individual level, 1 puppy, 3 juveniles, and 2 adolescents performed significantly above chance overall (at least 8/10, binomial test, $p = .043$).

Relationships to detector dog performance

Delayed-response. Figure 5-5 shows performance across delays as a function of outcome for each age group. There was no effect of outcome on performance in puppies, $F(1,13) = .028, p = .870$. There was no overall effect of outcome for juveniles, $F(1,18) = .052, p = .822$, but suitable candidates were above chance at the 10-s delay, $t(12) = 2.92, p = .013$, while unsuitable candidates were above chance at 60-s delay, $t(6) = 2.5, p = .047$. In the adolescent group, suitable candidates were above chance at all delays ($ps < .016$), while unsuitable candidates were only above chance at the 0-s and 10-s delays, ($ps < .008$). There was a significant correlation between

the behavioral evaluation *Performance* component-scores and accuracy at the 40-s and 60-s delays, $r_s(72) = .356, p = .002$, and $r_s(72) = .255, p = .030$, respectively.

Object transpositions. There was no overall effect of outcome on accuracy in the object transpositions task for puppies, $F(1,14) = .068, p = .798$, juveniles, $F(1,18) = .423, p = .524$, or adolescents, $F(1,22) = .013, p = .910$. However puppies that were ultimately categorized as suitable performed below chance in the *double-cross switch* condition, $t(10) = -2.390, p = .038$. There were no significant correlations between performance on this task and behavioral evaluation component-scores.

Causality. Figure 5-4 shows an overall effect of outcome on accuracy, $F(1, 54) = 5.824, p = .019$. Post hoc tests revealed that differences were not significant between the two outcome groups for puppies, $t(14) = 1.047, p = .313$, or adolescents, $t(22) = .812, p = .425$, but for juveniles, suitable dogs had higher accuracies than unsuitable dogs, $t(17.99) = 3.068, p = .007$.

Discussion

The current study explored object-search abilities in candidate detection dogs targeting three different domains: object permanence, attention/working memory, and causal inference. We assessed the ontogenetic development of these abilities and evaluated performance on each task in relation to dogs' suitability as a detection dog. Overall, our results are in line with past findings that dogs' abilities to represent physical objects are limited, but undergo ontogenetic development similar to other species. Further, we found some evidence indicating that mechanisms related to successful detector dog performance may also facilitate dogs' ability to succeed in object-search tasks requiring understanding of the physical properties of objects. Notably, our odor control tests indicated that dogs were not using olfactory cues to locate the

hidden reward. Findings for each task are discussed separately, first in terms of developmental effects and next in the context of applications to working dog performance.

For the transpositions task, three types of object transpositions were conducted varying in degree of difficulty depending on whether or not the containers moved to new locations or substituted a previous location, and whether or not the containers crossed paths. To our knowledge, this is the first developmental investigation of dogs' performance on the transpositions task, and only the second study of the ontogeny of object permanence in dogs. We found a significant interaction between transposition type and age, in which successful performance was only evident in the 11-mo group at the simplest level. In terms of development, this finding coincides with the age at which dogs in Gagnon & Doré (1994) succeeded in an invisible displacement task. Consistent with several other studies, dogs had difficulty with more complex transpositions and were only successful in the simplest condition in which objects moved to a new location and did not cross paths (Doré et al., 1996; Fiset & Plourde, 2013; Rooijakkers et al., 2009). This replicates findings by Rooijakkers et al. (2009), who systematically examined the factors that affect performance on transpositions and found that container crossing and substitution greatly impeded dogs' ability to track the object in the correct container, whereas great apes were unaffected. Indeed, we found no difference in performance between the second and third levels, both of which involved container crossing which seems to be the greatest factor affecting dogs' performance on this task (Rooijakkers et al., 2009). Further, like Rooijakkers et al. (2009) and Doré et al. (1996), we also found that when both substitution and crossing factors were combined at the most difficult level, dogs reverted to choosing the location where the reward was last seen, as evidenced by below-chance responding in this condition. Interestingly, despite not being successful in locating the reward in any condition,

puppies also used this strategy in the most difficult condition. This suggests that, although puppies lacked the ability to follow the trajectory of the moving hidden objects, their behavior was apparently under control of where they had last seen the object. Doing so presumably requires object permanence, corresponding to Piaget's stage 4 (Gagnon & Doré, 1994). Overall, these findings indicate that like object permanence, performance on transpositions, at least at the simplest level, improves with age and emerges by 11 months. Future research is needed to determine whether this capacity might appear between 6 and 11 months as we did not test dogs within that range, but we can assume no further improvements would have occurred had we tested older dogs given that Rooijackers et al. (2009) tested adults ranging from 1-10 years old and found no effect of age. Finally, our results corroborate other studies concluding that dogs have difficulty on invisible displacement and object transposition tasks (Doré et al., 1996; Fiset & Plourde, 2013; Rooijackers et al., 2009), and that the specific ontogenetic experiences undergone by detection dog training do not facilitate earlier or more advanced development of such skills.

In the delayed-response task, dogs were required to solve visible displacement tasks after delays of 0, 10, 40, and 60 seconds. We found a significant effect of age where 11-month olds performed above chance at each delay, puppies did not perform above chance on any delay, and juveniles' performance vacillated between chance and above-chance levels across delays. Performance in the oldest group showed a similar pattern to one other study using a similar procedure with adult dogs (Fiset et al., 2003), in which accuracy was high at short delays and gradually declined, but remained above chance, between 10 and 60 seconds. Given the contrasting performance between our youngest and oldest age group, and variable performance in the intermediate age group, we can postulate that the ability to succeed in a delayed-response

task with delays of up to 60 s is not yet solidified by 3 months of age in puppies, but begins to develop somewhere around 6 months and is fully established by 11 months. Due to methodological features of our task, we are cautious to attribute performance to extents or limitations of working memory. That is, while it is certainly possible that working memory played a role in dogs' ability to locate the reward after a delay, we did not attempt to isolate the process of working memory. In order for a spatial procedure to strictly test working memory, the ability to use other cues such as body orientation or gaze direction towards the location of the target needs to be prevented. Some studies have attempted to control for such strategies by introducing a screen to block the dogs' view of the locations; however, this would only prevent gaze fixation on the target location and does not control for the ability to orient towards the general location. Because no other studies have investigated spatial working memory in young dogs, we wanted to maximize dogs' possibility of success and reduce the chance of making the task too difficult that it would mask any developmental differences. Thus, we cannot conclude that performance on this task solely reflected working memory. However, given that the oldest group showed a typical memory function as delays increased and a similar pattern to Fiset et al. (2003) who did block dogs' visual access during the delay, it is likely that working memory indeed played a role in this group's performance. Nevertheless, though we did not quantify behavior during the delay, we did observe that some individuals fixated on the correct location during the delay. Thus, the ability to sustain attention across the longer delays likely also played a role. Given the significant overlap in neural mechanisms underlying attention and working memory systems, and the critical role of attention in successful working memory performance (Reynolds & Romano, 2016), it is likely that performance relied on interactions between both systems. Notably, neither of the two younger groups performed above chance at the 0-s delay.

Given that these trials were effectively tests of visible displacement object permanence, which is reported to develop by 8 weeks in puppies (Gagnon & Doré, 1994), it is surprising that puppies had difficulty in this condition. However, to avoid any cueing by the experimenter, the puppy was not released until the experimenter returned to the start position next to the handler and puppy. This was done due to previous reports that when the experimenter remains behind the containers, dogs are biased towards the position nearest the experimenter (Fiset & LeBlanc, 2007; Rooijackers et al., 2009). The trade-off for this is that waiting for the experimenter to return to the start position imposed a slight delay, and the movement of the experimenter towards the dog may have been distracting. Given that all dogs were tested in the same way, these factors apparently only affected younger puppies and not the 11-mo olds. Further, we found that puppies committed significantly more non-responses (i.e., failed to choose any container within 15 s) than either of the two older groups, suggesting that other factors such as distractibility and motivation had a greater effect in younger puppies. Future studies using delayed-response tasks should attempt to control or identify these factors; for example, eliminating human involvement in the movement of the objects, controlling for perceptual cueing during delays (e.g., re-orientation during delays), and monitoring subjects' behavior during the day using eye-tracking or physiological measures which may be informative of the role of processes like attention, arousal, and motivation.

In the casual reasoning task, dogs did not observe which container was baited with the reward and instead were required to locate the reward based on the sounds produced by shaking the baited and empty cups, inferring that a rattling sound would indicate a reward inside whereas no sound would indicate that it was empty. We found no effects of age on performance, and overall found that dogs failed to locate the reward based on the causal auditory cues. This finding

is consistent with that of Bräuer et al. (2006), which suggested that dogs' performance on such tasks was not based on causal understanding of the cues. Despite poor group performance, 1 puppy, 3 juveniles, and 2 adolescents were significantly above chance in choosing the correct container at the individual level. However, Bräuer et al. (2006) found that dogs were simply attracted to containers that produced noise, even when no causal relationships were present. We did not include a control condition for attraction to noise, and so we cannot conclude whether these individual dogs responded based on casual understanding or simply due to attraction to the noisy container. Oddly, 1 juvenile and 2 adolescents chose the empty container significantly above chance. In our procedure, the experimenter manipulated both containers on each trial and sessions were counterbalanced for which side (left or right) was baited; thus, we can rule out the influence of human actions or side biasing, leaving unclear what would lead these dogs to choose the silent container.

In addition to developmental effects, we also assessed whether performance on each task was associated with, and predictive of, suitability as a detection dog. In order to determine the earliest age at which cognitive abilities might be predictive of future success, we analyzed performance as a function of eventual outcome separately for each age group. For the transpositions task, we only found predictive performance in the youngest group. Specifically, below-chance performance on the *double-cross switch* position was predictive of detector dog suitability. Because the containers switched places on these trials, below-chance performance indicates preference for the container where the reward was originally placed before it was moved. Therefore, this effect may be explained by dogs' motivation and focus for the reward, coupled with dogs' limited ability to follow complex transpositions. That is, below-chance performance on this condition likely reflected greater motivation for the toy in future successful

puppies, which led to their attempt to locate the toy as best they could. Indeed, motivation and desire to chase an object or play with a toy are reportedly critical predictors of working dog success (Jamieson et al., 2017; Rooney et al., 2004). However, performance on the task was not predictive of suitability in the two older groups. One possibility is that this difference seen in the youngest group reflects dogs' inherent behavioral characteristics that are less apparent with maturation and training. Nevertheless, indications that early cognitive performance may hint at future success provides a promising foundation for further investigating potential cognitive markers of working dog success.

Performance on the delayed-response task was predictive of outcome in the oldest group in that future suitable dogs remained significantly above chance at all delays, whereas future unsuitable dogs fell to chance levels on the 40- and 60-s delays. Again, this difference in performance likely reflects stronger desire for the reward in suitable dogs, allowing them to withstand longer delays compared to weaker dogs. However, performance in the 6-mo group was less straightforward in terms of its' value in predicting outcome; in this group, only dogs that would succeed in the program performed significantly above chance on the 10-s delay, but the opposite was true at the 60-s delay where only *unsuccessful* dogs performed above chance. This result seemingly contradicts our explanation based on motivation, but may reflect other processes such as arousal. For example, Bray et al. (2015) found that like in humans, dogs' performance on difficult cognitive tasks was affected by arousal; specifically, excitable dogs experienced decrements in performance when arousal was artificially increased. A similar phenomenon may account for the pattern observed on the delayed-response task, with arousal interfering with performance in the longer and more difficult delays; however, along with this interpretation and Bray et al. (2015) findings, the arousal (elicited by the sight and then

disappearance of the toy along with restraint during the interval) only interfered with performance in the more excitable dogs (i.e., more excited by the toy), which were those that were more successful in the long run due to a greater desire for the reward. Thus, it may not be working memory per se that is predictive of dogs' performance as a detector dog, but the mechanisms that facilitate or interfere with performance on such tasks such as attention, motivation, and arousal. The fact that performance in the youngest puppy group was not predictive of future outcome is not surprising given our findings that puppies overall had difficulty on this task. In addition to performance as a function of outcome, we also found a weak but significant correlation between composite scores for *Performance* and accuracy on the 40- and 60-s delays. This component-score was derived from several detection-related behaviors including dogs' ability to focus and hunt independently, as well as their inherent desire and motivation to perform tasks and obtain the reward. Thus, it is not surprising that behaviors related to attention and motivation were at least somewhat associated with dogs' ability to sustain performance over the longer delays.

Finally, we found few associations between performance on the causal reasoning task and detector dog performance or suitability, which is likely the result of dogs' failure overall on this task. However as reported above, six dogs spanning the three age groups performed above chance at the individual level. All six of these dogs were ultimately categorized as suitable. Further, in the juvenile group suitable dogs performed significantly better than unsuitable dogs. This may again indicate that stronger desire for the reward, which enabled dogs to be successful detector dogs, also facilitated their ability to locate the reward by enhancing sensitivity to cues that indicates its location.

Taken together, these results support the hypothesis that dogs' understanding of the physical world necessary for locating hidden objects by inferring their location using visual or causal cues is limited, which may result from the loss of these skills throughout dogs' evolution. Overall, the literature suggests that dogs are inferior to great apes in their understanding of the physical world, but dog-wolf differences appear to be task-dependent; thus, phylogenetic factors influencing physical cognition may have affected different physical problem-solving domains differently. In the current study, we focused on ontogenetic rather than phylogenetic development as this aspect has been seldom addressed. We predicted that the experiences of candidate detector dog puppies, which involves object play and exploration and engages advanced cognitive processes such as spatial navigation and memory, might enhance the skills necessary for physical problem-solving. However, this prediction was not supported as we did not find evidence for the early emergence of these abilities and found that dogs' performance was limited and comparable to reports in other canid dog populations. Along these lines, Müller et al. (2016) found no effect of prolonged early exposure to toys designed for learning about physical contingencies on subsequent understanding of principles such as size constancy, physical support, solidity, and gravity in pet dogs. These findings along with those of the current study suggest that passive experiences with the physical world are not enough to enable advanced physical problem-solving abilities, or that specific experiences may be context-specific and do not result in learning rules that transfer to other domains (Müller et al., 2016). However, it remains to be seen whether explicit training with the objects and contingencies involved in testing can result in such transfer.

An important point that has been raised is that conclusions about dogs' limitations on visual object-tracking tasks must be interpreted with caution, taking into account the sensory

modality and ecological relevance of the task (Fiset & Plourde, 2013; Rooijakkers et al., 2009). That is, dogs are not primarily visual animals and rely predominantly on their sense of smell. As such, it is difficult to imagine that either domestication or experience would equip dogs with the ability to spontaneously solve visually-based tasks. This may also have influenced performance in the current study if the dogs' attempted to use their sense of smell, as they had been trained to do, which may have interfered with attention to visual stimuli. As recommended, it would be more appropriate to test dogs on equivalent olfactory-based tasks (Rooijakkers et al., 2009), though it is hard to conceptualize how one could test for principles such as invisible displacement and causality using odors. An alternative and valuable future study would be to instead examine object-search abilities in dogs selectively bred and trained for visually-based tasks; for example, although the dogs in our study consisted of Labrador retrievers, a breed initially designed and utilized to assist hunters in retrieving game birds, other modern uses have produced different lines diverging from this original purpose leading to vast within-breed variability in behavioral (and morphological) profiles. Many breeds, including Labradors, now consist of pet, show, and working lines, with variation even within working lines (e.g., assistance, emotional support, scent detection) producing dogs with distinct temperaments suited for the nature of the particular task (Fadel et al., 2016). Labrador retrievers bred for detection work, such as those in the current study, have been selected for air-scenting, trailing, and other olfactory abilities taking precedence over the visual sense. Selection for these traits is a slight but distinct departure from Labradors used in hunt and field trials, which are required to visually "mark" several locations where different birds have fallen, remember their location in order to retrieve after a delay, and calculate the most efficient route. Thus, we might expect enhanced performance on visually-based physical problem-solving tasks in these dogs compared to those

within the same breed from different lines. Of course, differential performance between such groups of dogs may not necessarily be due to genetic selection for particular behavioral characteristics and could instead (or additionally) be the result of their corresponding training. Indeed, similar hypotheses about the relative effects of selection for breed-specific traits and related training and experience have been put forth to explain differences in the social and general problem-solving domains (Dorey et al., 2009; Konno et al., 2016; Marshall-Pescini et al., 2016). Future work controlling for breed group and experience will be needed to further clarify these effects.

In sum, we found age-related increases similar to other species in performance on tests of physical cognition, extending these findings to dogs. However, dogs' ability to locate hidden objects by inferring their location based on movement or causal cues was overall limited, which also supports hypotheses that the specific ecologies of dogs and possibly canids in general did not favor selection for these skills as assessed by traditional measures. We did not find evidence that potential cognitive enrichment fostered by scent detection training enhanced these abilities. However, we did find that some aspects of performance on physical problem-solving tasks, possibly reflecting mechanisms of attention and motivation, were predictive of detection dog success even at early ages. These findings contribute to the literature on the phylogenetic and ontogenetic origins of canine cognition, and have important applications to the working dog industry.

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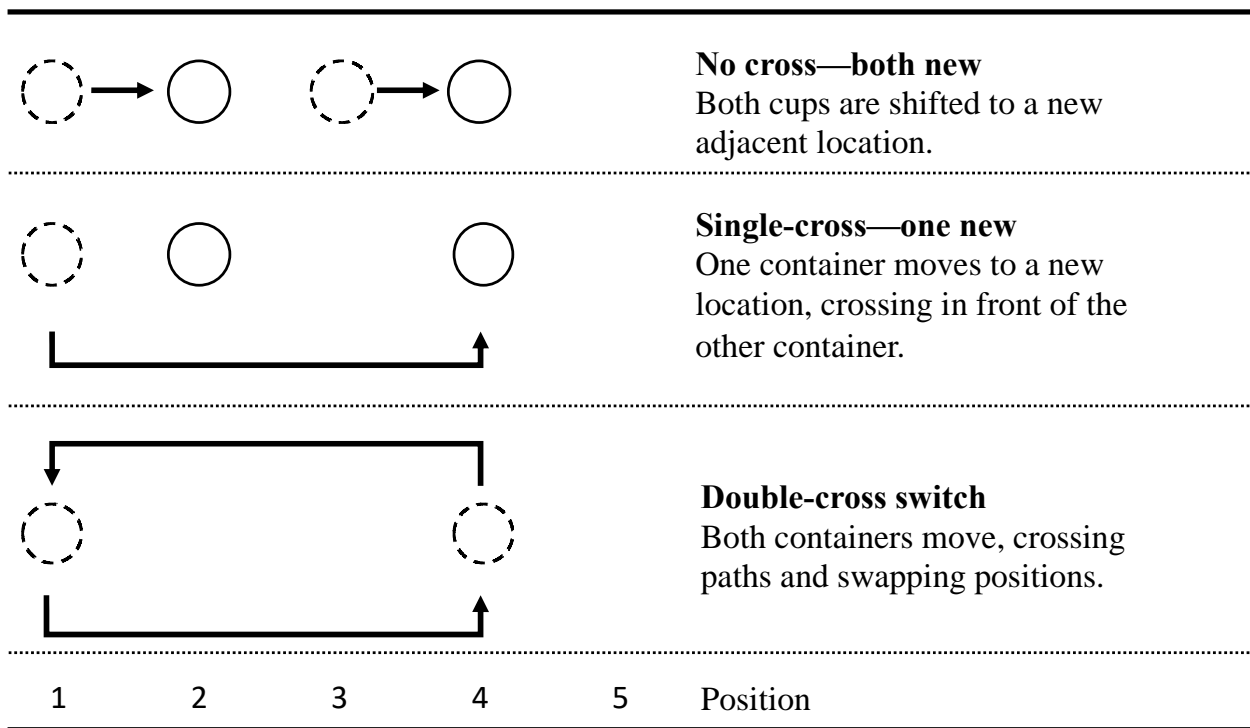


Figure 5-1. Schematic representation and description of the 3 types of transpositions performed in the current study, adapted from Rooijakkers et al., (2009). Arrows represent the movement of the containers in each condition from the start position (dashed circles) to end position (closed circles). Each condition contained four trials, counterbalancing the location of the reward (left or right container) and the direction of movement (left to right and right to left).

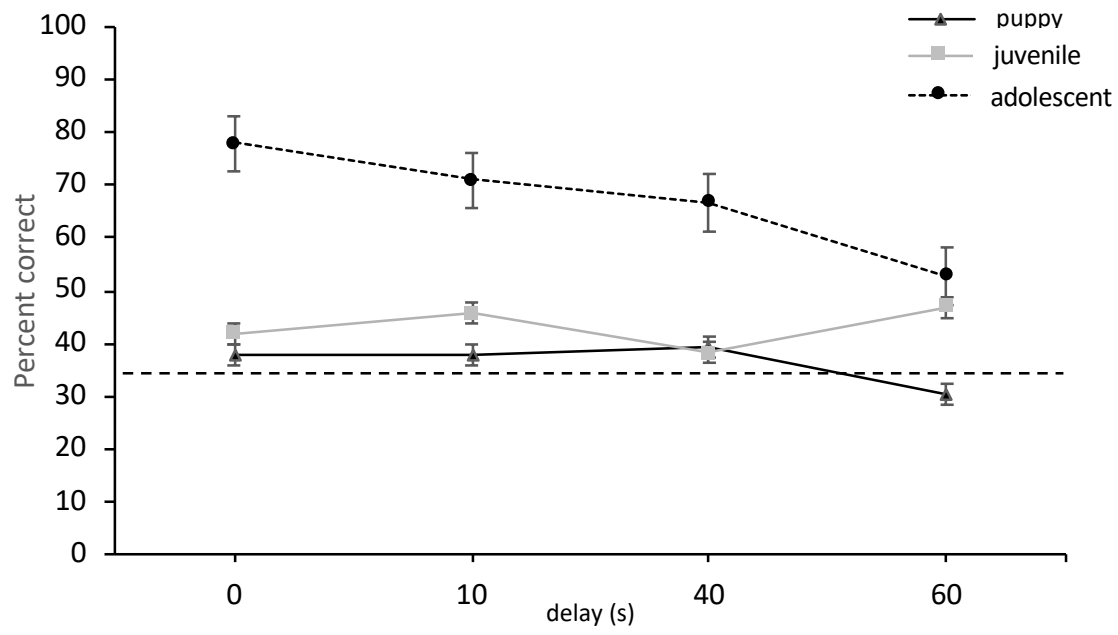


Figure 5-2. Average accuracy (percent correct) as a function of delay for each age group in the delayed-response task. Dashed line represents chance (33.33%).

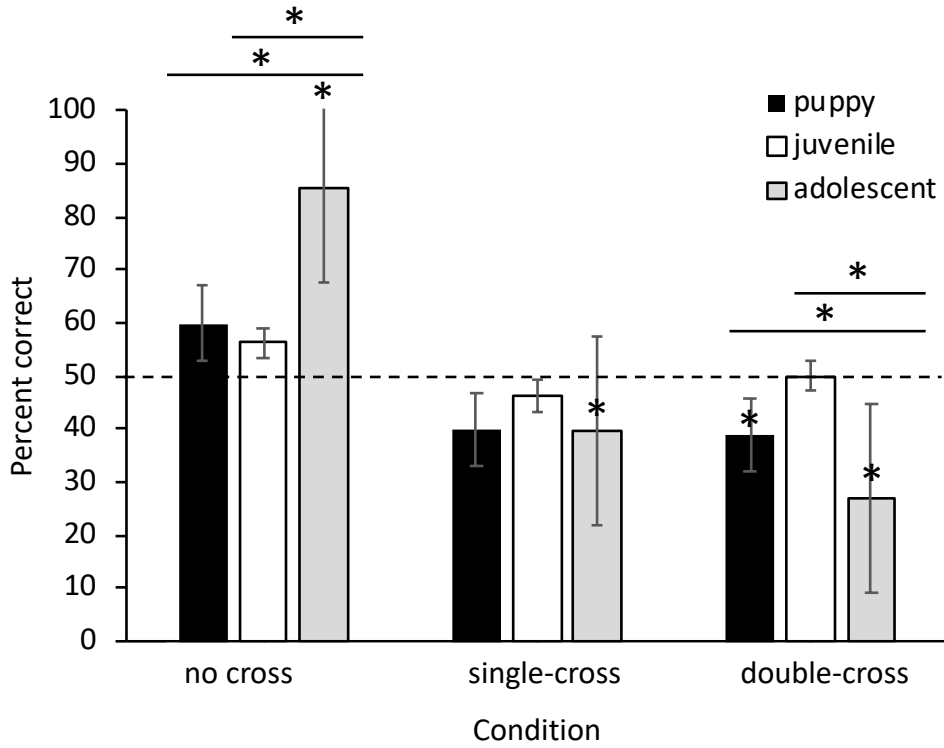


Figure 5-3. Average accuracy (percent correct) for each trial type of the transpositions task as a function of age. Dashed line represents chance (50%).

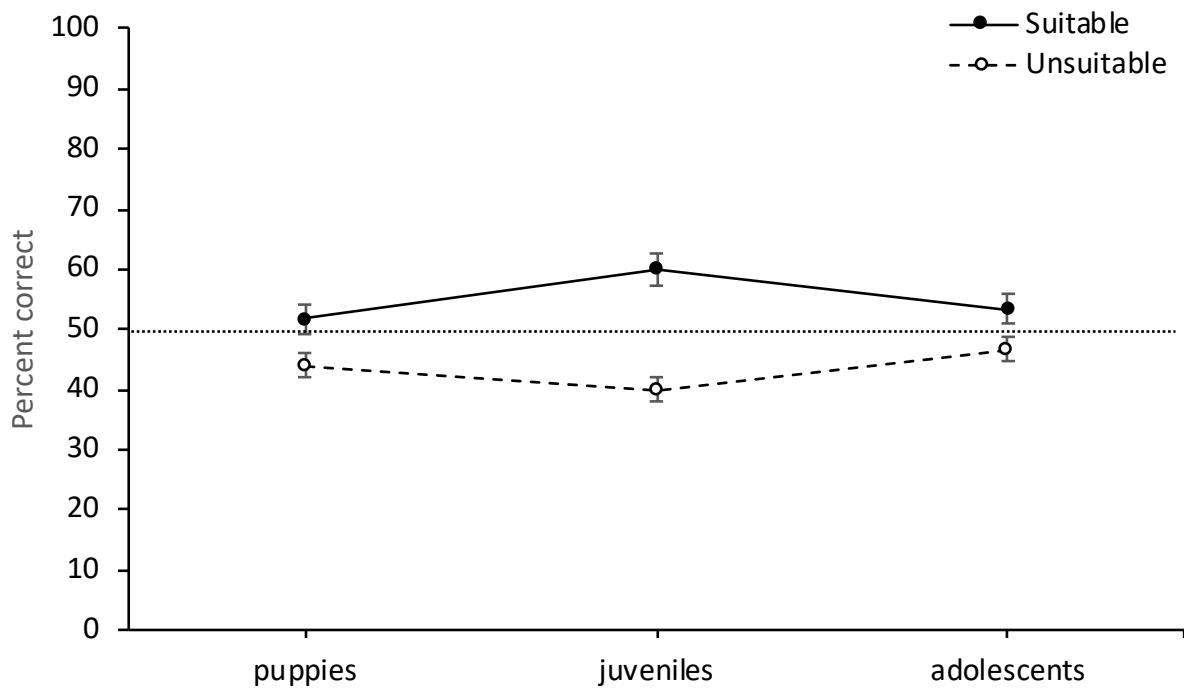


Figure 5-4. Average accuracy (percent correct) as a function of outcome for each age group in the causality task. Dotted line represents chance (50%).

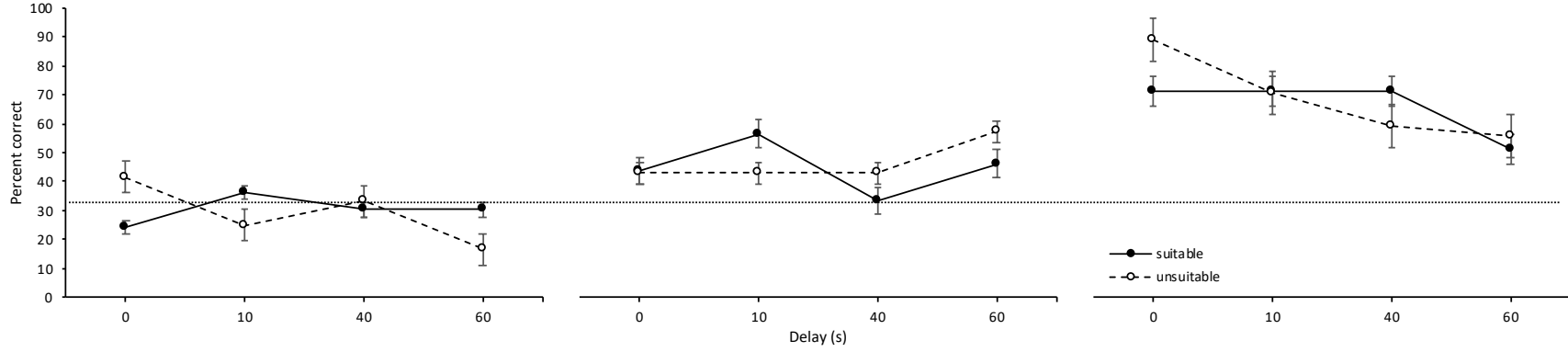


Figure 5-5. Average accuracy (percent correct) as a function of outcome for each age group (left panel: puppies; middle panel: juveniles; right panel: adolescents) in the delayed-response task. Dotted line represents chance (33.33%).

Chapter 6: Conclusions

Our understanding of the extents and limits of canine cognition, and corresponding assumptions about their implications for the origins of cognitive abilities, is rapidly broadening and reshaping. In this dissertation, I aimed to extend this knowledge to an underrepresented population of dogs by examining a diverse range of cognitive abilities in developing candidate detection dogs using a comprehensive suite of tests, and investigated their application to working dog selection. The research presented here provides an important comparison to existing reports in the literature in terms of ontogenetic and phylogenetic effects, advances our knowledge of early cognitive development in dogs, and provides a foundation for investigating cognitive markers of working dog success.

Chapter 2 describes the application of the Unsolvable Task for quantifying traditional behavioral characteristics important to working dog success, such as ‘drive’. Traditionally used as a measure of social cognition, and specifically human-directed gazing, I also investigated other non-social applications of this task such as persistence and problem-solving. Both task-oriented and human-directed gazing behaviors showed developmental increases, suggesting the importance of ontogenetic effects of experience with humans. Both variables were also associated with future detection dog suitability; overall, performance on the task reflecting independence, persistence, and engagement was indicative of detection dog trainability and success.

In Chapter 3, I explored the performance of detection dogs on the object-choice task, a widely used measure of dogs’ responsiveness to human signals. I modified the task to present conflicting social and olfactory cues in order to investigate biases towards one type of cue versus the other. Unlike extensive reports in the literature of dogs’ readiness in following human

pointing, detection dogs largely ignored the cue and located the reward based on scent. This finding again lends support to the hypothesis that ontogenetic effects greatly influence dogs' responsiveness to human social cues, showing that this behavior can actually be *reduced* due to specific experiences. Further, tendency to ignore the cue was predictive of detection dog success, which suggests that dogs' susceptibility to human biasing is an important factor in their suitability as a detection dog.

Chapter 4 investigated the development inhibitory control using two different measures of motor inhibition. Consistent with humans and other species, dogs also showed developmental increases in inhibitory control. Also consistent with other studies, performance on the two tasks did not correlate with each other, suggesting that inhibitory control is a multifaceted mechanism. Performance on both tasks were also predictive of detection dog suitability, but may be reflective of other general processes like motivation and neophobia rather than detection dog characteristics, per se.

Finally, in Chapter 5 I selected three tasks targeting dogs' object-search abilities reflecting object permanence and causal reasoning. Performance showed developmental increases similar to human children, but was generally mediocre which is in line with hypotheses that dogs exhibit reduced physical-problem solving skills compared to other species. However, individual performance reflected future detector dog suitability, which again may have been due to other motivational variables.

Overall, this dissertation highlights the importance of ontogenetic factors in the development of canine cognition, spanning various cognitive domains. These results contribute to the comparative literature of cognitive development, extending and diversifying the representation of the domesticated dog population. Importantly, these findings hint at the

significant role of cognition in working dog performance and may lay the foundation for necessary improvements in selection.

Appendix

Rotated Structure Matrix for PCA with Varimax Rotation of a Two Component Scale

Items	Rotated Component Coefficients		Communalities
	Component 1	Component 2	
Focus	.921	.237	.875
Hunt	.918	.177	.904
Work effort	.915	.220	.578
Air scenting	.907	.170	.721
Independence	.806	.265	.886
Possession	.760	-.025	.852
Vehicles/urban clutter	.196	.922	.724
People	.156	.881	.800
Surfaces	.127	.842	.889

Note. major loadings for each item are bolded.