Executive functions in detection dogs

Sarah Krichbaum

A dissertation submitted to the Graduate Faculty of
Auburn University
in partial fulfillment of the
requirements for the Degree of
Doctor of Philosophy

Auburn, Alabama
August 7, 2021

Keywords: executive functions, working memory, inhibitory control, detection dogs

Approved by

Jeffrey Katz, Chair, Professor, Department of Psychological Sciences
Lucia Lazarowski, Research Scientist, Canine Performance Sciences, Assistant Research Professor, Department of Anatomy, Physiology, and Pharmacology
Chris Newland, Professor, Department of Psychological Sciences
Jennifer Robinson, Professor, Department of Psychological Sciences
Melissa Singletary, Assistant Director, Canine Performance Sciences, Assistant Professor, Department of Anatomy, Physiology, and Pharmacology
Paul Waggoner, Co-Director, Canine Performance Sciences, Adjunct Associate Professor, Department of Anatomy, Physiology, and Pharmacology

Abstract

Researchers in the field of canine cognition have developed several tasks to study executive functions, like working memory and inhibitory control, in dogs. Findings from such tasks have provided new information regarding the evolution, welfare, and aging of man's best friend as well as the relationship between cognition and suitability in specific roles (e.g., working dogs). However, it remains important to understand factors that produce the individual differences that are common to these tasks and clearly define the constructs that the tasks are measuring. In this dissertation, I explore executive functions in detection dogs. Chapter 2 evaluates dog working memory for odors using the delayed matching-to-sample task and raises questions regarding how task specific features, including stimulus modality, influence results. Chapter 3 explores the internal validity of the visible displacement task, commonly used to measure working memory in dogs, and suggests the use of a necessary control in future research. Finally, Chapter 4 follows a two-fold focus. First, the relationship between cognitive tasks to measure executive functions in dogs is assessed. Second, the ability of these tasks to predict detection dog suitability is evaluated. Together, the results stress the importance of considering the validity of tasks purported to measure executive functions in dogs and provides evidence of factors that can influence task performance. In addition, the findings represent a clear relationship between tasks used to measure executive function (namely working memory and inhibitory control) and aspects of detection dog suitability, suggesting their value as non-traditional evaluation measures. Combining this information with behavioral, genetic, and physiological data could provide a multifaceted approach to predicting detection dog success.

Acknowledgements

This research was made possible by several people who supported me in this long but rewarding journey. First, I would like to thank my advisor, Dr. Jeffrey Katz for mentorship throughout the entire process. The experiments within were designed carefully and meticulously with his help. He was consistently troubleshooting and answering questions regarding methods, data, and interpreting results. Aside from this, he was a constant supporter (calling me every time we got the good news of a grant or publication) and friend.

I would also like to thank the staff and trainers at Canine Performance Sciences for welcoming me and my research. They frequently aided in the logistics, dog support, and dog training that allowed these projects to run smoothly. Specifically, I want to thank Dr. Paul Waggoner and Dr. Lucia Lazarowski for encouraging words that usually were comprised of "that sounds like an interesting idea, we will try to help make it happen". Their attitude always reassured me that this process was worthwhile.

To my lab mates, who are now my lifelong friends and colleagues. I could not thank you enough for the long hours that you volunteered to help conduct these studies. Although I am sure you were never pleased to see the "can you possibly help me run dogs on Saturday morning?" text pop up on your phone, you always showed up and gave it your all. Your knowledge of the dogs and their quirks was valuable in experimental design and discussions. Cheers to you all!

Thanks to the BEST participants that one could ask for. This dissertation would not have been possible without the dogs that loved to learn and play. I can honestly say that these *pawticipants* were always up to the task, which I am sure was mostly due to that fact that it ended with balls and treats. The small moments with these pups that made me laugh and (sometimes) cry will be treasured memories. And to my own dogs, Vera (who was a participant

and then adopted) and Akela who laid on my lap, typically one on each side, nearly every time I sat down to try and write this dissertation. Honestly, their love inspired me to keep pressing on even on the hardest days.

To my mom, dad, and brother for the thousands of phone calls about graduate school, its ups and downs, my successes and failures, and everything in between. Mom, thanks for teaching me to never stop asking “why?”. That lesson helped me design these experiments, come up with creative analyses, and brainstorm explanations for the results. Dad, thanks for instilling in me the idea that you always start your day by “putting your thinking cap on”. This attitude got me through the many weekends of data collection that I thought would never end. John, thank you for visits and Facetime calls that brought much needed laughter and a reminder about what is truly important. I sincerely would not have been able to do this without you all.

Finally, to my best friend and partner, Luke. I cannot thank you enough for standing by my side during this process. You listened to every frustration and were the calm voice that I could rely on to say, “everything is going to be okay”. I loved how you treated every small triumph as if it were cause for celebration. Your positivity is without match. Thank you for making me dinner when I was hangry, listening to me rehearse my dissertation defense over and over again, being my shoulder to cry on, and making me smile. Your help, in every way possible, is so greatly appreciated.

Table of Contents

List of Tables

List of Figures

Chapter 1: General Introduction

Canine cognition was birthed over 100 years ago, when ideas from Pavlov's work on conditioned reflexes were merged with Thorndike's research on animal intelligence (Feurbacher & Wynne, 2011). However, the field was slow to become the thriving and rigorous science that it is today due to feelings that the wide diversity of dogs caused by domestication would prevent clear findings (De Waal, 2016). When the study of canine cognition was building steam in the late 1990's, it seemed to occur without any specific driving force (Feurbacher & Wynne, 2011). However, researchers agree that a portion of the "rise of dogs" was due to the formation of unique theories regarding how dogs became socialized parts of our homes and society (Feurbacher & Wynne, 2011; Mikósi, 2015). The question was whether dogs' unique roles arose from domestication due to social pressures (Hare et al., 2002) or socialization and training with humans (Udell, Dorey, and Wynne, 2010), however, it is widely accepted that genetic changes (or phylogeny) as well as social experiences (or ontogeny) produced the keen social abilities of dogs that make them engrained in our everyday lives (Lazarowski et al., 2020a; Udell et al., 2010). Following arguments that the field of canine cognition had a narrow focus on social aspects and was lacking empirical studies on non-social cognition (Bensky et al., 2013), researchers began to expand their domestication theories to tests of problem-solving (Müller et al., 2016).

It was posited that selection of dogs as pets made them more reliant on humans for needs that would have once required certain problem-solving abilities (e.g., navigating hunting terrain) and decreased their capacity for non-social cognitive skills (Müller et al., 2016; Udell et al., 2010). Considering this idea, comparative researchers reported differences in wolves and dogs on tasks used to measure aspects of non-social cognition. For example, wolves outperformed dogs on measures of persistence (Brubaker et al., 2017; Rao et al., 2018, Udell, 2015) and problem solving (Udell, 2015) but displayed no difference on measures of behavioral flexibility, or the ability to adapt one's behavior in a changing environment (Brucks et al., 2019; Olsen et al., 2018). However, dogs outperformed wolves on measures of inhibitory control (Range et al., 2020). These mixed results call for an increased effort to understand how different groups of dogs use non-social cognition to solve complex tasks.

Although research has suggested that non-social cognition abilities may be limited in the domestic dog, most of the studies focused on pets. Given that pet dogs are only one portion of the population of domestic dogs, their abilities should not be generalized. For example, working dogs have the potential to develop specific cognitive skills based on experience that is non-existent in pet dogs (Lazarowski et al., 2020a). In addition, although working dogs play multiple roles in our society, from guide dogs to narcotics and explosive detection, their non-social cognition is often overlooked and understudied (Bensky, 2013). Working dogs require exquisite problem-solving abilities to successfully complete their work (from navigating complex environments to remembering odors) making them an ideal candidate for the study of higher-order non-social cognition, such as executive functioning (Lazarowski et al., 2020a; Lit, 2009; Maclean and Hare, 2018; Troisi et al., 2019).

Executive functions can be defined as top-down mental processes that require the effortful use of skills such as working memory and inhibitory control (Diamond et al., 2013). While the definition of human working memory remains a topic of debate that is beyond the scope of this dissertation (see Cowan, 2016 for a review), in non-humans it can be more simply defined as short-term memory for stimuli within a specific experimental trial or session (Honig, 1978; Olton & Samuelson, 1976). Inhibitory control, a *somewhat* more translational construct, can be defined as inhibiting a prepotent response for a more appropriate alternative (Diamond, 2013; Olsen, 2018). Recent studies on executive functions in dogs (see Olson, 2018 for review), have discovered that processes such as working memory and inhibitory control can be easily measured with short cognitive tasks. These tasks have led to findings regarding the evolution, welfare, and aging of dogs as well as the relationship between executive functions and working dog suitability (Brady et al., 2018; Bray et al., 2014; Bray et al., 2020; Bray et al., 2021; Hare & Ferrans, 2021; Kelly et al., 2019; Lazarowski et al., 2020a; Maclean & Hare, 2018; Tiira et al., 2020).

This research may be particularly important for detection dogs. First, studies have indicated that detection dogs are the most effective method for finding explosives (Helton, 2009) and their need is increasing (Lazarowski et al., 2020b; Leighton et al., 2018; Otto et al., 2019). With nearly a 50 percent drop-out rate in training programs (Cobb et al., 2014) it is necessary to find early predictors of detection dog suitability (Brady et al., 2018). Second, early studies of executive functions in detection dogs suggest that performance on certain cognitive tasks can predict detection dog success and stress the importance of developing new and valid measures (Brady et al., 2018; Lazarowski et al., 2020a; Maclean and Hare, 2018; Tiira et al., 2020). For example, Maclean and Hare (2018) found that a measure of working memory was positively related to program outcome and Lazarowski and colleagues (2020a) found that although performance on the same task did not predict program outcome in detection dog puppies, it did positively relate to training evaluation scores on performance in 3-mo old puppies and training evaluation scores for environmental soundness in 6-mo old's (Lazarowki et al., 2020a). The increasing need for detection dogs combined with evidence of a link between executive functions and detection work stresses the importance of studying executive functions in dogs. While the use of these tasks to predict program success has been fruitful, their validity is unfortunately lacking.

The visible displacement task (VDT) is the most common task to assess working memory in detection dogs. While the VDT can be used to predict detection dog success (Lazarowski et al, 2020a; Maclean and Hare, 2018) there are two important limitations. First, this task is specific to spatial working memory, leaving out information regarding other stimulus modalities, such as olfaction, that may have more specific implications for detection dog work (Hayes et al., 2018). Second, there is a major confound that continually raises questions regarding the internal validity of the VDT. For example, dogs can use non-mnemonic strategies, such as sustained attention and head or body orientation to solve the task without relying on memory mechanisms (Adams et al., 2000). To uncover a more focused view of working memory, it is important to implement tasks with other stimulus modalities as well as address confounds that could influence the tasks' ability to accurately predict detection dog success.

Multiple studies have displayed the poor construct validity of tasks purported to assess executive functions such as inhibitory control evidenced by the lack of cross-task correlations (Bray et al., 2014, Brucks et al., 2017; Fagnani et al., 2016; Vernoullit et al., 2018). In addition, studies exploring performance on how inhibitory control tasks relate to detection dog suitability display conflicting findings show poor predictive validity. For example, Tiira and colleagues (2020) found that dogs that displayed better inhibitory control found more explosives in an area search task, while others found no relationship between performance on the same task and detection dog success (Maclean & Hare, 2018; Lazarowski et al., 2020a). Although it is possible that these tasks are measuring different aspects of inhibitory control (Reimer et al., 2014), these results must be considered when discussing the relationship between inhibitory control and detection dog work.

In summary, current work on executive functions in dogs is limited to the visuospatial stimulus modality in pets. Although there are few studies that assess these skills in non-pet populations, including working dogs, they lack the validity that is necessary when discussing implications of the results. This dissertation will fill major gaps in the current literature. First, studying the limits of dogs olfactory working memory will provide new knowledge on the working memory abilities of dogs and allow for a cross modality comparison. Second, assessing the validity of executive function tasks to measure working memory and inhibitory control will offer insight on what these tasks are measuring as well as their relationship to detection dog suitability.

Dissertation Outline

The goal of this dissertation is two-fold. First, the information gained here will fill gaps in the canine cognition literature regarding the validity of common tasks used to evaluate executive functions in dogs. Second, the relationship between performance on these tasks and detection dog suitability will be determined. Chapter 2 implements the delayed matching-to-sample task with odors to investigate the effect of factors, such as stimulus modality and interference, on the duration of dog working memory. Chapter 3 evaluates how the use of non-mnemonic strategies effects performance on the VDT. Chapter 4 focuses on the relationships among tasks used to measure executive functions in dogs, including tasks purported to measure inhibitory control (Spatial Discounting Test and Cylinder Task), working memory and attention (VDT) and explores the relationship between performance on these tasks and detection dog suitability. Chapter 5 summarizes the findings in relation to the validity of the tasks used to measure executive functions in dogs as well as specific implications for detection dog work.

References

Adams, B., Chan, A., Callahan, H., Siwak, C., Tapp, D., Ikeda-Douglas, C., Atkinson, P., Head, E., Cotman, C. W., & Milgram, N. W. (2000). Use of a delayed non-matching to position task to model age-dependent cognitive decline in the dog. *Behavioural Brain Research*, *108*(1), 47–56. https://doi.org/10.1016/S0166-4328(99)00132-1

Bensky, M. K., Gosling, S. D., & Sinn, D. L. (2013). The world from a dog's point of view: a review and synthesis of dog cognition research. In *Advances in the Study of Behavior* (Vol. 45, pp. 209-406). Academic Press.

Brady, K., Cracknell, N., Zulch, H., & Mills, D. S. (2018). Factors associated with long-term success in working police dogs. *Applied Animal Behaviour Science*, *207*, 67–72. https://doi.org/10.1016/j.applanim.2018.07.003

Bray, E. E., Gruen, M. E., Gnanadesikan, G. E., Horschler, D. J., Levy, K. M., Kennedy, B. S., ... & MacLean, E. L. (2020). Cognitive characteristics of 8-to 10-week-old assistance dog puppies. *Animal Behaviour*, *166*, 193-206. https://doi.org/10.1016/j.anbehav.2020.05.019

Bray, E. E., MacLean, E. L., & Hare, B. A. (2014). Context specificity of inhibitory control in dogs. *Animal Cognition*, *17*(1), 15–31. https://doi.org/10.1007/s10071-013-0633-z

Bray, E. E., Otto, C. M., Udell, M. A., Hall, N. J., Johnston, A. M., & MacLean, E. L. (2021). Enhancing the Selection and Performance of Working Dogs. *Frontiers in Veterinary Science*, *8*, 430. https://doi.org/10.3389/fvets.2021.644431

Brubaker, L., Dasgupta, S., Bhattacharjee, D., Bhadra, A., & Udell, M. A. R. (2017). Differences in problem-solving between canid populations: Do domestication and lifetime experience affect persistence? *Animal Cognition*, *20*(4), 717–723. https://doi.org/10.1007/s10071-017-1093-7

Brucks, D., Marshall-Pescini, S., & Range, F. (2019). Dogs and wolves do not differ in their inhibitory control abilities in a non-social test battery. *Animal Cognition*, *22*(1), 1–15. https://doi.org/10.1007/s10071-018-1216-9

Brucks, D., Marshall-Pescini, S., Wallis, L. J., Huber, L., & Range, F. (2017). Measures of Dogs' Inhibitory Control Abilities Do Not Correlate across Tasks. *Frontiers in Psychology*, *8*. https://doi.org/10.3389/fpsyg.2017.00849

Cobb, M., Branson, N., McGreevy, P., Lill, A., & Bennett, P. (2015). The advent of canine performance science: Offering a sustainable future for working dogs. *Behavioural Processes*, *110*, 96–104. https://doi.org/10.1016/j.beproc.2014.10.012

Cowan, N. (2017). The many faces of working memory and short-term storage. *Psychonomic Bulletin & Review*, *24*(4), 1158-1170. https://doi.org/10.3758/s13423-016-1191-6

De Waal, F. (2016). *Are we smart enough to know how smart animals are?*. WW Norton & Company.

Diamond, A. (2013). Executive Functions. *Annual Review of Psychology*, *64*, 135–168. https://doi.org/10.1146/annurev-psych-113011-143750

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

Feuerbacher, E. N., & Wynne, C. D. L. (2011). A history of dogs as subjects in North American experimental psychological research. *Comparative Cognition & Behavior Reviews*, *6*, 46–71. https://doi.org/10.3819/ccbr.2011.60001

Hare, B., Brown, M., Williamson, C., & Tomasello, M. (2002). The domestication of social cognition in dogs. *Science (New York, N.Y.)*, *298*(5598), 1634–1636. https://doi.org/10.1126/science.1072702

Hare, B., & Ferrans, M. (2021). Is cognition the secret to working dog success?. *Animal Cognition*, 1-7. https://doi.org/10.1007/s10071-021-01491-7

Hayes, J. E., McGreevy, P. D., Forbes, S. L., Laing, G., & Stuetz, R. M. (2018). Critical review of dog detection and the influences of physiology, training, and analytical methodologies. *Talanta*, *185*, 499–512. https://doi.org/10.1016/j.talanta.2018.04.010

Helton, W. S. (Ed.). (2009). *Canine ergonomics: The science of working dogs*. CRC Press/Taylor & Francis.

Honig, W. K. (1978). Studies of working memory in the pigeon. *Cognitive processes in animal behavior*, *211*, 248.

Kelly, D. M., Adolphe, J. L., Vernouillet, A., McCausland, J. A., Rankovic, A., & Verbrugghe, A. (2019). Motoric self-regulation by sled dogs and pet dogs and the acute effect of carbohydrate source in sled dogs. *Animal Cognition*, *22*(6), 931–946. https://doi.org/10.1007/s10071-019-01285-y

Lazarowski, L., Krichbaum, S., Waggoner, L. P., & Katz, J. S. (2020a). The development of problem-solving abilities in a population of candidate detection dogs (Canis familiaris). *Animal Cognition*. https://doi.org/10.1007/s10071-020-01387-y

Lazarowski, L., Waggoner, L. P., Krichbaum, S., Singletary, M., Haney, P., Rogers, B., & Angle, C. (2020b). Selecting Dogs for Explosives Detection: Behavioral Characteristics. *Frontiers in Veterinary Science*, *7*, 597. https://doi.org/10.3389/fvets.2020.00597

Leighton, E., Hare, L., Thomas, S., Waggoner, L., & Otto, C. (2018). A solution for the shortage of detection dogs: A detector dog Center of Excellence and a Cooperative Breeding Program. *Frontiers in Veterinary Science*, *5*, 284. https://doi.org/10.3389/fvets.2018.00284

Lit, L. (2009). Evaluating Learning Tasks Commonly Applied in Detection Dog Training. In *Canine Ergonomics: The Science of Working Dogs* (pp. 99–114). https://doi.org/10.1201/9781420079920.ch6

MacLean, E. L., & Hare, B. (2018). Enhanced Selection of Assistance and Explosive Detection Dogs Using Cognitive Measures. *Frontiers in Veterinary Science*, *5*.

Miklósi, Á. (2015). *Dog behaviour, evolution, and cognition* (2nd ed.). Oxford University Press. https://doi.org/10.3389/fvets.2018.00236

Müller, C. A., Riemer, S., Virányi, Z., Huber, L., & Range, F. (2016). Inhibitory Control, but Not Prolonged Object-Related Experience Appears to Affect Physical Problem-Solving Performance of Pet Dogs. *PLOS ONE*, *11*(2), e0147753. https://doi.org/10.1371/journal.pone.0147753

Olsen, M. R. (2018). A case for methodological overhaul and increased study of executive function in the domestic dog (Canis lupus familiaris). *Animal Cognition*, *21*(2), 175–195. https://doi.org/10.1007/s10071-018-1162-6

Olton, D. S., & Samuelson, R. J. (1976). Remembrance of places passed: Spatial memory in rats. *Journal of Experimental Psychology: Animal Behavior Processes*, *2*(2), 97–116. https://doi.org/10.1037/0097-7403.2.2.97

Otto, C. M., Cobb, M. L., & Wilsson, E. (2019). Editorial: Working Dogs: Form and Function. *Frontiers in Veterinary Science*, *6*. https://doi.org/10.3389/fvets.2019.00351

Range, F., Brucks, D., & Virányi, Z. (2020). Dogs wait longer for better rewards than wolves in a delay of gratification task: But why? *Animal Cognition*. https://doi.org/10.1007/s10071-020-01346-7

Rao, A., Bernasconi, L., Lazzaroni, M., Marshall-Pescini, S., & Range, F. (2018). Differences in persistence between dogs and wolves in an unsolvable task in the absence of humans. *PeerJ*, *6*. https://doi.org/10.7717/peerj.5944

Riemer, S., Mills, D. S., & Wright, H. (2014). Impulsive for life? The nature of long-term impulsivity in domestic dogs. *Animal Cognition*, *17*(3), 815–819. https://doi.org/10.1007/s10071-013-0701-4

Tiira, K., Tikkanen, A., & Vainio, O. (2020). Inhibitory control – Important trait for explosive detection performance in police dogs? *Applied Animal Behaviour Science*, 104942. https://doi.org/10.1016/j.applanim.2020.104942

Troisi, C. A., Mills, D. S., Wilkinson, A., & Zulch, H. E. (2019). Behavioral and cognitive factors that affect the success of scent detection dogs. *Comparative Cognition & Behavior Review*, *14*, 51-76. https://doi.org/10.3819/CCBR.2019.140007

Udell, M. A. R. (2015). When dogs look back: Inhibition of independent problem-solving behaviour in domestic dogs (*Canis lupus familiaris*) compared with wolves (*Canis lupus*). *Biology Letters*, *11*(9), 20150489. https://doi.org/10.1098/rsbl.2015.0489

Udell, M. A. R., Dorey, N. R., & Wynne, C. D. L. (2010). What did domestication do to dogs? A new account of dogs' sensitivity to human actions. *Biological Reviews of the Cambridge Philosophical Society*, *85*(2), 327–345. https://doi.org/10.1111/j.1469-185X.2009.00104.x

Vernouillet, A. A. A., Stiles, L. R., Andrew McCausland, J., & Kelly, D. M. (2018). Individual performance across motoric self-regulation tasks are not correlated for pet dogs. *Learning & Behavior*, *46*(4), 522–536. https://doi.org/10.3758/s13420-018-0354-x

Chapter 2: Dissociating the effects of delay and interference on dog (*Canis familiaris*) working memory

Published in Animal Cognition:

Krichbaum, S., Lazarowski, L., Davila, A., Cox, E., Smith G. J., Waggoner L. P., Katz, J. S. (2021). Dissociating the effects of time and interference on dog working memory. *Animal Cognition.* https://doi.org/10.1007/s10071-021-01509-0

Abstract

Delayed matching-to-sample (dMTS) is commonly used to study working memory (WM) processes in non-humans. Previous procedures for studying dog WM, including versions of the dMTS, did not separate the impact of delay and interference on memory performance. These studies were also limited to auditory and spatial stimuli, neglecting dogs' dominant sensory modality (i.e., olfaction). Therefore, we designed the first olfactory dMTS in dogs, with systematically varied delays and number of odors in a session, to dissociate the effects of delay and within-session proactive interference on dog WM. Dogs (n = 5) initially trained on matching-to-sample with 48 odors, with a zero-second delay, were tested on four delay lengths (0, 30, 60, and 90 seconds), counterbalanced across three, trial-unique, sessions. Although there was a slight decrease in accuracy across delays, dogs performed above chance on delays up to 60 seconds, suggesting a WM duration of at least 60 seconds. To explore the effect of within-session proactive interference on WM duration, the size of the stimulus set was reduced to six and two odors. There was no effect on the memory function with six odors compared to the trial-unique sessions. However, the interference caused by the two-odor set was enough to decrease accuracy at each delay length. These findings suggest that forgetting in dog working memory for odors can be simultaneously influenced by delay and within-session proactive interference.

Keywords: working memory, delayed matching-to-sample, dog, olfaction

Introduction

Working memory (WM) in non-humans is often defined as short-term memory for stimuli within a specific experimental trial or session (Honig, 1978; Olton & Samuelson, 1976), and is commonly measured as the duration (i.e., the amount of time) that an animal can remember a stimulus during a task. The most well-known and often implemented task used to study WM in non-humans is the delayed matching-to-sample (dMTS) task (e.g., Shettleworth, 2009; Wright, 2012). The dMTS is a variation of the MTS task in which a subject is presented with a single sample stimulus, followed by its removal and then a delay period. After the delay, the subject is presented with two comparison stimuli, one that matches the sample and another that does not. A response to the matching comparison is reinforced. The task is considered to evaluate WM because the subject is required to retain information regarding the sample stimulus for the duration of the delay to make a correct choice. Therefore, WM duration is measured as the longest delay at which above-chance performance is maintained (Lind, Enquist, & Ghirlanda, 2015).

In addition to delay, the number of times stimuli repeat in a single session can influence dMTS performance. This type of interference, called within-session proactive interference, occurs when memory for earlier events in the session influences memory for later ones (Wright, 2012). For example, monkeys were tested on a two-choice, visual dMTS, with stimuli set sizes of either 100 or two images in 50-trial sessions. The results indicated that monkeys performed above chance on delays up to 24 hours with the 100-image set but were only successful on delays up to a few seconds with the two-image set (Overman & Doty, 1980). While these results show that monkeys can remember images for extended periods of time in some conditions, they also reflect the simultaneous effects of delay and within-session proactive interference on monkeys' WM duration. A critical aspect of this study is that the images in the 100-item set were trial-unique, meaning that the matching and non-matching images on every trial in the session never repeated. Therefore, the experimenters created a condition in which within-session proactive interference was essentially non-existent (Wright, 2012). These results suggest that the decrease in performance across delays in the trial-unique sessions represent the effect of delay while the decrease in performance caused by the reduced set size represents the combined effects of delay and within-session proactive interference (Overman & Doty, 1980; Wright, 2012).

Researchers have tested many species on versions of the dMTS that require memory of spatial, visual, and auditory stimuli (Lind et al., 2015). A recent review that compared cross-species performance on different versions of the dMTS showed that mammals typically outperform non-mammals. For example, all species that displayed a performance half-life (i.e., the delay that results in performance falling half-way between zero delay performance and chance) of over one minute were mammals. In addition, no species displayed a half-life over 300 seconds (Lind et al., 2015). While these results could be interpreted as the absolute limits of these species' WM abilities, it is important to consider the level of within-session proactive interference that each animal encountered during testing before discerning if the forgetting was due to delay, within-session proactive interference, or a mixture of the two.

In addition to within-session proactive interference, other factors such as modality of the stimuli can influence dMTS results (Shettleworth, 2009; Wright, 2012). Stimulus modality is particularly related to memorability as stimuli that are processed by the animal's dominant sensory system are likely to be more salient. For example, studies found that while rats (Iversen, 1997; Iversen, 1993) and dogs (Martucci & Swindell, 2014) were unable to form a conditional identity relation with visual stimuli, they were successful with the more dominant, olfactory stimuli (rats: Peña, Pitts, & Galizio, 2006; dogs: Lazarowski et al., 2021). Lind et al. (2015) suggest that previous results from variations of the dMTS could be split into two categories: specialized (i.e., memory related to the animal's needs) and general (i.e., memory for biologically neutral stimuli); the latter being similar across species and lasting only seconds to a few minutes and the former lasting far longer in some cases. Therefore, it is important to recognize the relevance of the stimuli to the species when discussing dMTS results.

In past studies, dogs were tested on versions of the dMTS task that focused on WM for spatial and auditory stimuli (Adams et al., 2000a; Adams et al., 2000b; Chan et al., 2002; Head et al., 1995; Kuœmierek & Kowalska, 2002; Milgram et al., 1994; Tapp et al., 2003; Zanghi et al., 2015). The most common is the visual delay non-matching-to-position task (vDNMP) that is used to study the effects of aging on dogs' WM, a growing area of study due to evidence suggesting that the brain of aging dogs displays similar deficits as humans with neurodegenerative diseases (Adams et al., 2000a; Adams et al., 2000b; Chan et al., 2002; Head et al., 1995; Milgram et al., 1994; Tapp et al., 2003; Zanghi et al., 2015). The vDNMP is a variant of the non-MTS task in which a dog is presented with an object on either the left or right side of a tray. After the dog displaces the object and receives a food reward, the tray is removed, and a variable delay occurs. Following the delay, the tray is reintroduced to the dog with identical objects on both the left and right side. A response of displacing the object on the side opposite of the sample position is reinforced. Results from a similar three-choice design show that seemingly healthy dogs are accurate at choosing the correct position following delays of 110 seconds, even with the large amounts of within-session proactive interference produced by using the same three positions across 12-trial sessions, while aged dogs only remained accurate following delays of 30 seconds (Chan et al., 2002).

In a variation of the procedure used to evaluate dog WM for auditory stimuli, dogs were presented with a sound from a center speaker, centered within an operant chamber. Following a delay, either a matching or non-matching sound was presented from one of the side speakers (Kuœmierek & Kowalska, 2002). A response (lever press) on the matching trials but not the non-matching trials was reinforced. After meeting a training criterion, delays were inserted between presentation of a sound in the center speaker and presentation of a sound from one of the side speakers. In contrast to the vDNMP, the auditory dMTS had essentially no within-session proactive interference with trial-unique stimuli but dogs only performed accurately for a up to a one-minute delay (Kuœmierek & Kowalska, 2002).

Due to variations in dMTS results across stimulus modalities and the lack of experimental data reporting on dog WM for odors, we created the first olfactory dMTS in dogs. Based on the results of previous studies using spatial and auditory stimuli (Chan et al., 2002; Kuœmierek & Kowalska, 2002), as well as the previous argument that olfaction is dogs' dominant sensory modality (Hayes, 2018), we hypothesized that although dogs would display a decrease in accuracy across delays, they would maintain above-chance accuracy on the highest delay tested (90 seconds). In addition, the prior studies did not systematically vary within-session proactive interference. Therefore, following the delay sessions, we decreased the set size to properly dissociate the effects of delay and within-session proactive interference on WM performance. We hypothesized that, like other species, dogs' performance would decrease as a function of decreasing set size but would not interact with delay, suggesting independent but simultaneous effects of the two factors on dogs' WM (see Wright, Kelly & Katz, 2018 for a review).

Methods

Subjects

Five purpose-bred detection dogs (*Canis familiaris*) from the Auburn University Canine Performance Science Program were used in this study. The dogs were Labrador retrievers and varied in age (*M* = 3.98) and sex (Females = 3, Males = 2). Ethical approval was granted by the Auburn University Institutional Care and Use Committee (protocol number #2018-3334). Each dog was previously trained on odor detection and were equally familiar with the odors in this task (Lazarowski et al., 2021). Experimental sessions occurred four times a week.

Apparatus

All training and testing sessions occurred in an enclosed area in a building at the Canine Performance Science Center. The enclosed area (6.5 x 6 m) consisted of three sections (A, B, C) formed by dividers made of plywood (see Fig 1). Inside the arena (section A), six, 19 x 19 x 19 cm cinderblocks with an open end facing upwards, were placed on 28 x 28 x 18 cm wooden blocks arranged in a semi-circle formation, 0.45 m apart, and equidistant (2.7 m) from the center of the arena opening which served as choice positions. On the left-side (section B), outside of the arena, three, 19 x 19 x 19 cm cinderblocks, with an open end facing upwards, were placed on 28 x 28 x 18 cm wooden blocks which served as sample positions and were adjacent to the dog's start position. The handler (in section B), experimenter 1 (in section C) and experimenter 2 (outside of the enclosed area, to the left of section B) viewed the trials on a monitor and were out of the dog's view while the dog was in the arena. A GoPro Hero 5 camera was used to live stream and record all sessions.

Stimuli

Odor stimuli were cotton pads (Swisspers® 100% cotton rounds pads) that were scented by storing them in airtight glass jars with approximately 28 g of one of 48 different household spices and essential oils for a minimum of one week (see Table 1 for complete list of odors). Before each session, the cotton pads were transferred to stimulus tins (6 cm in diameter) with metal tweezers with the experimenter using nitrile gloves. The tins were perforated with nine, 2 mm holes for odor release. The tins were placed in open, pint-sized paint cans so that they fit securely in the cinderblocks.

Task

Acclimation. The dogs in this study were previously trained on a two-choice olfactory MTS task (Lazarowski et al., 2021). Prior to dMTS test sessions, two, trial-unique, sessions, consisting of 24 trials, were conducted to acclimate the dogs to the delay procedure (i.e., maintaining the dog on a short leash in the arena opening for the duration of the delay). The 48 odors were selected without replacement, so each odor occurred as either an S+ or S- once per session. Acclimation sessions consisted of six delays (0, 15, 30, 45, 60, and 75 seconds) that were counterbalanced for delay such that each delay occurred four times throughout the session. In addition, the position of the matching (S+) and non-matching (S-) odors were counterbalanced across the six positions in the arena such that each appeared in each position four times throughout the session. The other four positions remained empty.

On every trial, the dog remained outside of the arena (section B) while experimenter 1 set up the sample and comparison odors. Then the dog was required to investigate the sample odor in one of the three cinderblocks (sample positions) located outside of the arena until a characteristic change in behavior noted as odor recognition was observed by the handler (Lazarowski et al., 2021). Three sample positions were used to encourage search behavior, as pilot work indicated some dogs would rapidly pass by a single sample position. Upon sampling, the handler moved the dog to the arena opening using a tab leash. Directly after the dog was moved to the arena opening, experimenter 1 removed the sample odor from the cinderblock outside of the arena. Experimenter 2 began the timer when the sample odor was removed and said “okay” when the delay time was met, which cued the handler to drop the leash, allowing the dog to enter the arena. The handler, blind to the positions of the S+ and S-, lifted her hand to indicate that the dog made a response (defined as the dog’s nose coming within 5 cm of the top of a cinderblock and sitting). If the dog responded to the S+, experimenter 2 said “yes”, the handler marked the response with a clicker, cueing the dog to exit the arena and receive a ball as reinforcement. If the dog responded to the S-, experimenter 2 said “no”, and the handler called the dog to exit the arena. The dogs were required to meet an acclimation criterion of a minimum of 75% correct on zero-delay trials combined across the two sessions to ensure that they were motivated to complete the entire session, which was nearly 45 minutes in length. Upon meeting the acclimation criteria dogs began the trial-unique dMTS test.

Trial-unique dMTS test. The effect of delay on WM duration was first assessed across three, trial-unique, dMTS test sessions which occurred in the same manner as dMTS acclimation but consisted of four delays (0, 30, 60, and 90 seconds) across the 24 trials (six trials per delay). In addition to delay and position of the S+ and S-, the sessions were also counterbalanced for whether the S+ occurred to the left or right of the S-. We hypothesized that if dogs were tracking the position of the S+ odor during the delay, they would encounter the S+ first significantly more than chance, therefore, each session was scored to determine whether the dog encountered (defined as the dog’s nose coming within 5-cm of the top of the cinderblock) the S+ or S- first on each trial. A built in zero-delay criterion, to control for factors such as motivation or fatigue, required that the dogs were 83.33% correct on zero-delay trials. If a dog failed to meet the zero-delay criteria on any session, the session was repeated.

Within-session proactive interference tests. The effect of within-session proactive interference on WM duration was assessed by reducing the number of stimuli (set size) that occurred in each session to six or two odors, with three sessions per set size. The order of set size tests was counterbalanced across dogs such that three dogs completed three sessions with six odors and then three sessions with two odors and two dogs completed three sessions with two odors first. Each odor appeared four times as an S+ and S- in sessions consisting of six odors and twelve times as an S+ and S- in sessions consisting of two odors and were counterbalanced for choice position. Within-session proactive interference test sessions were identical to the trial-unique dMTS test sessions consisting of four delays (0, 30, 60, and 90 seconds) across the 24 trials (six trials per delay); however, dogs were not expected to meet a zero-delay criterion.

Data analysis. To ensure that dogs were not tracking the position of the S+ during the delay, we conducted a binomial test that compared the number of trials that each dog encountered the S+ first to chance (12 trials) immediately following each session and compared the number of trials that each dog encountered the S+ first on average across all testing sessions using a one-sample *t*-test. We used a generalized linear mixed-effects model (GLMM) with individual dog ID as a random factor and binomial family distribution (lme4 package; Bates et al., 2015) to determine accuracy (correct = 1; incorrect = 0) as a function of delay (0, 30, 60, 90) and set size (2, 6, 48). Session order (1, 2, 3) and trial number (1 to 24) were included as additional fixed factors to assess performance across and within sessions, as well as their interactions with delay and set size. We also compared average performance on each delay for each set size to chance (50%) using a series of one-sample *t*-tests.

Results

All dogs met the dMTS acclimation criteria and, on average, performed significantly better than the criteria of 75% correct on zero-delay trials (*M* = 85, *SE* = 0.03) combined across the two acclimation sessions ($t(4) = 3.98$, $p = 0.016$, $d = 1.75$). Two dogs repeated the first trial-unique dMTS test session and one dog repeated the second trial-unique dMTS test session due to failure to meet the zero-delay criterion. On average, the dogs did not encounter the S+ first significantly more than chance ($t(4) = -0.39$, $p = 0.72$, $d = -0.43$). However, one dog encountered the S+ first significantly more than chance (binomial < 0.05) on the second trial-unique dMTS test session, therefore, that session was repeated, and she was required to remain in section C during delays for that session and all sessions remaining to eliminate the possibility of scent tracking.

Figure 2 depicts a significant decrease in accuracy across delays (GLMM: $z = -5.11$, $p < 0.001$, odd ratio (*OR*) = 166.33, 95 % CL 165.67, 167.00) and a significant effect of set size such that accuracy was higher on the trial-unique (48) and six-odor sets compared to the two-odor set (GLMM: $z = 3.07$, $p = 0.002$, $OR = 21.54$, 95% CL 15.21, 29.90; $z = 2.49$, $p = 0.013$, $OR = 12.061$, 95% CL 8.69, 16.75). There was no effect of session order or trial number and no significant interactions (GLMM: *p*'s > 0.06). A series of one-sample *t*-tests revealed that, with 48- and six-odor sets, dogs performed significantly above chance on delays up to 60 seconds (48: $t(4) = 8.55$, $p = 0.001$, $d = 8.55$; 6: $t(4) = 3.72$, $p = 0.02$, $d = 3.72$), but not 90 seconds (48: $t(4) = 2.89$, $p = 0.05$, $d = 1.29$; 6: $t(4) = 2.59$, $p = 0.06$, $d = 1.16$). With the two-odor set, dogs were only above chance on zero-second delays ($t(4) = 3.65$, $p = 0.022$, $d = 3.65$).

Discussion

Dogs demonstrated high levels of performance on delays up to 60 seconds on the 48 (67.78%) and six-odor sets (67.78%). However, when only two odors occurred in the session and each odor was encountered on every trial, compared to only one and eight times in the other set sizes, dogs only performed above chance on zero-second delays (72.22%). In addition, there was a slight decrease in performance across delays and an effect of set size such that dogs performed better on the 48 and six-odor sets than the two-odor set. These results depict a delay function and within-session proactive interference effects that are common to dMTS (e.g., see Wright, 2012 and Wright, Kelly, & Katz, 2018 for reviews) and are the first representation of olfactory dMTS in dogs.

Comparing WM duration on the 48 and smaller six and two-odor sets allowed us to dissociate the effects of delay and within-session proactive interference on the memory function (Wright, 2012). When within-session proactive interference was non-existent (trial-unique, 48-odor set) dogs displayed a decrease in accuracy that could be attributed to delay and created the necessary baseline to examine the effects of proactive inference (Wright, 2012). While there was no difference in performance between the 48 and six-odor sets, the within-session proactive interference caused by the two-odor set did decrease performance at each delay length. Therefore, within-session proactive interference caused an overall decrease in performance (intercept) but did not interact with delay (slope) suggesting the two factors were isolated via systematic variation of delay and the number of odors in a session. In the present task, dog olfactory WM duration was at least 60 seconds and no more than 90 seconds. The effect of proactive interference was prominent in the two-odor set but dissipated in the six-odor set.

While dogs displayed a qualitatively similar delay function to previous studies on WM duration in dogs (Chan et al., 2002; Kuœmierek & Kowalska, 2002), the maximum duration of WM (60 sec) was lower than the reported duration of WM on the vDNMP (110 sec), but similar to that reported on the auditory dMTS task (60 sec). This was surprising, as we hypothesized that dogs would perform above chance on the highest delay tested (90 sec) due to the dominance of dogs' olfactory ability. One explanation for the shorter duration could be the small sample size (n=5) in relationship to studies using the vDNMP (n=17; Chan et al., 2002). It is possible that increasing the sample size could increase the size of the effect.

However, the longer duration on the vDNMP could be due to the use of non-mnemonic strategies that are not possible in the olfactory dMTS. For example, a persistent confound on the vDNMP is that dogs can use non-mnemonic strategies, such as orienting their head or body in the direction of the correct (non-matching) stimulus position, throughout the delay, to solve the task (Fiset et al., 2003). Chan et al. (2002) attempted to account for this problem by designing a three-choice task in which the non-matching stimulus could be in one of two locations following the delay. However, it remains possible that dogs could orient towards the sample stimulus position during the delay and then choose the stimulus that appeared in either adjacent position to the one they are orienting following the delay. This important confound could explain why dogs in these tasks performed above chance at longer delays than dogs in the current study. Future research should clearly dissociate the use of non-mnemonic strategies and WM in spatial WM tasks.

While it is possible that the current findings elucidate the absolute limits of dogs WM duration, additional studies are necessary before applying these results to other breeds and working dogs especially those that rely on scent matching (e.g., tracking dogs). For example, there is evidence that the act of searching, or locomotion facilitates detection ability and could effectively increase WM in these cases (Gadbois & Reeve, 2014). Alternatively, tracking dogs may be reintroduced to the "sample" odor periodically throughout the tracking process allowing them to work successfully for far longer than their WM allows or due to the nature of the task (i.e., tracking a single odor for an extended period) the odor could be transferred to long term memory storage. Future studies should implement the olfactory dMTS in applied settings to determine the extent to which context, reintroduction of the sample odor, and other memory processes, influence matching ability.

Conclusion

This study demonstrated the first dMTS task to assess olfactory WM in dogs and dissociated the effects of delay and within-session proactive interference by systematically varying delays and number of odors in a session. When within-session proactive interference was controlled (trial-unique, 48 odor set) dogs displayed above chance performance on up to 60 seconds. These results suggest that dogs have WM for odors of at least 60 seconds. However, when within-session proactive interference was introduced by decreasing the stimulus set size to two-odors, performance decreased at each delay length. This evidence contributes to a theoretical framework for discussing the combined effects of delay and within-session proactive interference on non-human WM. It also provides new information regarding dog olfactory WM duration that builds upon related work on dog olfactory WM capacity (Krichbaum et al., 2020). It remains important to evaluate across species comparisons on WM tasks; however, due to differences in the relevance of stimuli and other task-specific features, assessing the validity of tasks used to measure WM is best done within a single species (Lind et al., 2015; Miklósi et al., 2015). Once such functional relationships have been established within a species, then similar procedures can be compared across species to understand the evolution of WM as well as its important applications (e.g., the study of aging).

References

Adams, B., Chan, A., Callahan, H., & Milgram, N. W. (2000a). The canine as a model of human cognitive aging: Recent developments. *Progress in Neuro-Psychopharmacology & Biological Psychiatry*, *24*(5), 675–692. https://doi.org/10.1016/s0278-5846(00)00101-9

Adams, Beth, Chan, A., Callahan, H., Siwak, C., Tapp, D., Ikeda-Douglas, C., Atkinson, P., Head, E., Cotman, C. W., & Milgram, N. W. (2000b). Use of a delayed non-matching to position task to model age-dependent cognitive decline in the dog. *Behavioural Brain Research*, *108*(1), 47–56. https://doi.org/10.1016/S0166-4328(99)00132-1

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software*, *67*(1), 1–48. https://doi.org/10.18637/jss.v067.i01

Chan, A. D. F., Nippak, P. M. D., Murphey, H., Ikeda-Douglas, C. J., Muggenburg, B., Head, E., Cotman, C. W., & Milgram, N. W. (2002). Visuospatial impairments in aged canines (*Canis familiaris*): The role of cognitive-behavioral flexibility. *Behavioral Neuroscience*, *116*(3), 443–454. https://doi.org/10.1037/0735-7044.116.3.443

Fiset, S., Beaulieu, C., & Landry, F. (2003). Duration of dogs' (*Canis familiaris)* working memory in search for disappearing objects. *Animal Cognition*, *6*(1), 1–10. https://doi.org/10.1007/s10071-002-0157-4

Gadbois, S., & Reeve, C. (2014). Canine olfaction: scent, sign, and situation. In *Domestic dog cognition and behavior* (pp. 3-29). Springer, Berlin, Heidelberg.

Gagnon, S., & Doré, F. Y. (1994). Cross-sectional study of object permanence in domestic puppies (*Canis familiaris*). *Journal of Comparative Psychology*, *108*(3), 220–232. https://doi.org/10.1037/0735-7036.108.3.220

Hayes, J. E., McGreevy, P. D., Forbes, S. L., Laing, G., & Stuetz, R. M. (2018). Critical review of dog detection and the influences of physiology, training, and analytical methodologies. *Talanta*, *185*, 499-512. https://doi.org/10.1016/j.talanta.2018.04.010

Head, E., Mehta, R., Hartley, J., Kameka, M., Cummings, B. J., Cotman, C. W., Ruehl, W. W., & Milgram, N. W. (1995). Spatial learning and memory as a function of age in the dog. *Behavioral Neuroscience*, *109*(5), 851–858. https://doi.org/10.1037/0735-7044.109.5.851

Honig, W. K. (1978). Studies of working memory in the pigeon. *Cognitive Processes in Animal Behavior*, *211*, 248.

Iversen, I. (1997). Matching-to-sample Performance in Rats: A Case of Mistaken Identity? *Journal of the Experimental Analysis of Behavior*, *68*(1), 27–45. https://doi.org/10.1901/jeab.1997.68-27

Iversen, I. H. (1993). Acquisition of matching-to-sample performance in rats using visual stimuli on nose keys. *Journal of the Experimental Analysis of Behavior*, *59*(3), 471–482. https://doi.org/10.1901/jeab.1993.59-471

Kuœmierek, P., & Kowalska, D. M. (2002). Effect of sound source position on learning and performance of auditory delayed matching-to-sample task in dogs. *Acta Neurobiologiae Experimentalis*, *62*(4), 251-262.

Krichbaum, S., Rogers, B., Cox, E., Waggoner, L. P., & Katz, J. S. (2020). Odor span task in dogs (*Canis familiaris*). *Animal Cognition*. https://doi.org/10.1007/s10071-020-01362-7

Lazarowski, L., Davila, A., Krichbaum, S., Cox, E., Smith G. J., Waggoner L. P., Katz, J. (2021). Olfactory matching-to-sample abstract-concept learning by dogs (*Canis familiaris*). *Journal of Experimental Psychology: Animal Learning and Cognition.* Advance online publication. https://doi.org/10.1037/xan0000281

Lind, J., Enquist, M., & Ghirlanda, S. (2015). Animal memory: A review of delayed matching-to-sample data. *Behavioural Processes*, *117*, 52–58. https://doi.org/10.1016/j.beproc.2014.11.019

Martucci, K., & Swindell, S. (2014). *How Smart is Your Dog? An Experimental Analysis of Canine Learning Abilities* (Unpublished master's thesis). Washington State University, Pullman, WA. ttps://research.libraries.wsu.edu/xmlui/bitstream/handle/2376/5333/Martucci thesis.pdf?sequence=1

Miklósi, Á. (2015). *Dog behaviour, evolution, and cognition* (2nd ed.). Oxford University Press. https://doi.org/10.3389/fvets.2018.00236

Milgram, N. W., Head, E., Weiner, E., & Thomas, E. (1994). Cognitive functions and aging in the dog: Acquisition of nonspatial visual tasks. *Behavioral Neuroscience*, *108*(1), 57–68. https://doi.org/10.1037//0735-7044.108.1.57

Olton, D. S., & Samuelson, R. J. (1976). Remembrance of places passed: Spatial memory in rats. *Journal of Experimental Psychology: Animal Behavior Processes*, *2*(2), 97–116. https://doi.org/10.1037/0097-7403.2.2.97

Overman, W. H., & Doty, R. W. (1980). Prolonged visual memory in macaques and man. *Neuroscience*, *5*(11), 1825–1831. https://doi.org/10.1016/0306-4522(80)90032-9

Peña, T., Pitts, R. C., & Galizio, M. (2006). Identity matching-to-sample with olfactory stimuli in rats. *Journal of the Experimental Analysis of Behavior*, *85*(2), 203–221. https://doi.org/10.1901/jeab.2006.111-04

Shettleworth, S. J. (2009). *Cognition, evolution, and behavior*. Oxford University Press.

Tapp, P. D., Siwak, C. T., Estrada, J., Holowachuk, D., & Milgram, N. W. (2003). Effects of age on measures of complex working memory span in the beagle dog (Canis familiaris) using two versions of a spatial list learning paradigm. *Learning & Memory*, *10*(2), 148–160. https://doi.org/10.1101/lm.56503

Wright, A. A. (2012). *Memory processing.* In T. R. Zentall & E. A. Wasserman (Eds.), *The Oxford handbook of comparative cognition* (p. 239–260). Oxford University Press.

Wright, A. A., Kelly, D. M., & Katz, J. S. (2018). Comparing cognition by integrating concept learning, proactive interference, and list memory. *Learning & Behavior*, *46*(2), 107-123. https://doi.org/10.3758/s13420-018-0316-3

Zanghi, B. M., Araujo, J., & Milgram, N. W. (2015). Cognitive domains in the dog: Independence of working memory from object learning, selective attention, and motor learning. *Animal Cognition*, *18*(3), 789–800. https://doi.org/10.1007/s10071-015-0847-3

Table 1.

Complete list of 48 odor stimuli

Odor stimuli			
Allspice	Chamomile	Garlic	Pineapple
Almond	Champagne	Lemon	Raspberry
Amaretto	Cherry	Lime	Rootbeer
Anise	Cinnamon	Maple	Rosemary
Apple	Cloves	Marshmallow	Savory
Apricot	Coffee	Mustard	Strawberry
Blackberry	Coriander	Oregano	Sumac
Blueberry	Cotton Candy	Parsley	Tangerine
Butter	Eggnog	Peach	Thyme
Butterscotch	English Toffee	Peanut Butter	Tobacco
Caramel	Fennel	Pecan	Tumeric
Carob	Fenugreek	Pina colada	Watermelon

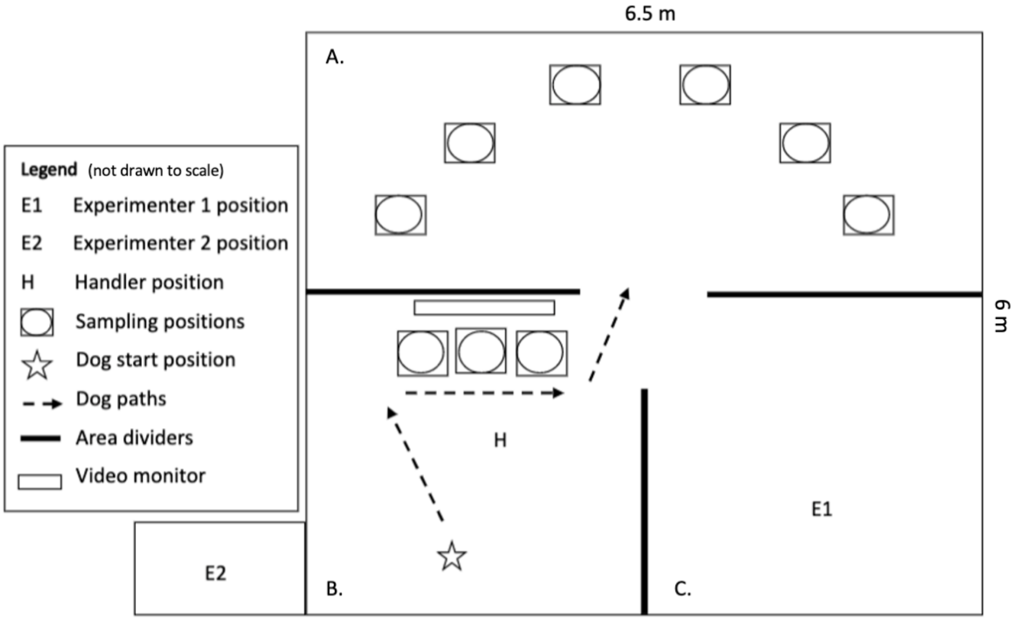


Figure 1. Schematic representation of experimental area. Dotted arrowhead lines show the pathway of the dog on each trial. After experimenter 1 (E1) set up the trial stimuli and returned to their position, the handler (H) directed the dog (starting from the start position indicated by the star) to begin the trial by investigating the three sampling positions (section B) until a perceptible recognition of odor in one of the positions was observed by the handler. Next, the dog was released into section A to investigate the six choice positions. The handler remained in section B observing the dog via a monitor transmitting a live feed of the enclosure and signaled when the dog made a response. Experimenter 2 (E2) remained outside the experimental area and confirmed whether the response was correct or incorrect and scored each trial.

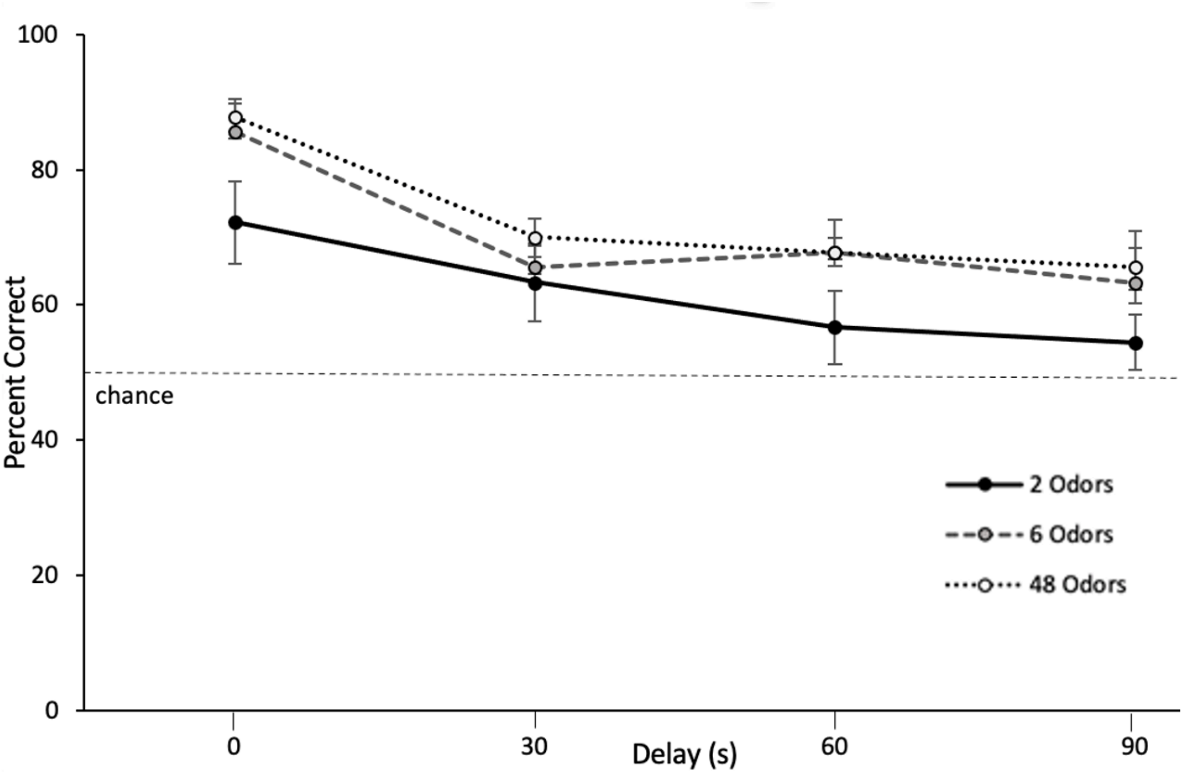


Figure 2. Average (+SEM) percent correct across delays for each odor set size (2, 6, 48). Dashed line represents chance (50%).

Chapter 3: Controlling for Dogs' (*Canis familiaris*) use of Non-Mnemonic Strategies in a Spatial Working Memory Task

Published in: Journal of Experimental Psychology: Animal Learning and Cognition

Krichbaum, S., Smith G. J., Lazarowski, L., Katz J. S. (in press). Controlling for dogs' (*Canis familiaris*) use of non-mnemonic strategies in a spatial working memory task. *Journal of Experimental Psychology: Animal Learning and Cognition.*

Abstract

Short assessments of spatial working memory (SWM) in dogs are becoming popular evaluations of canine aging and individual differences. In a typical SWM task an experimenter hides a reward inside of a bucket at a specific stimulus position while the dog watches. Then, following a varying delay interval, the dog is released to choose a bucket. The longest delay at which the dog can successfully choose the bucket containing the reward is considered to reflect the dog's SWM duration. Although past studies were informative, the tasks often lacked a valid measure of SWM due to dogs' ability to use non-mnemonic strategies, such as body orientation or sustained attention, to successfully solve these tasks without relying on working memory mechanisms. Therefore, we designed the first study to assess the internal validity of these tasks by directly comparing dogs' performance on two experimental conditions. We found that dogs performed worse in a control condition in which non-mnemonic strategies were eliminated compared to a typical SWM task condition. In addition, our results indicate a strong relationship between the percentage of delay time that a dog spends orienting their head or body to the correct bucket and performance in a typical SWM task. These findings were the first to show a difference in SWM performance when dogs' use of non-mnemonic strategies was controlled and stress the importance of considering the internal validity of these tasks if used to examine SWM in future work.

Keywords: non-mnemonic strategies, working memory, dogs

Introduction

Working memory (WM) or memory for stimuli within a short period of time (Honig, 1978; Olton & Samuelson, 1976), is an executive function that allows an animal to behave appropriately in changing environments and problem-solve (e.g., Baddeley, 2017). WM is typically measured in terms of duration or how long a specific stimulus can be remembered. While WM has been extensively studied in dozens of species (Shettleworth, 2009), the study of canine WM is currently rising due to findings that aging dogs undergo similar morphological and cognitive changes as aging humans (Olson, 2018). In addition, dogs hold multiple roles in our society, from companions to members of the workforce, all of which could benefit from a better understanding of the processes, like WM, that make dogs fit for specific roles (Bensky et al., 2013; Miklósi, 2015).

Due to discoveries that the aging dog brain displays similar deficits to that of humans, studying WM in dogs became useful as a translational account of aging (Adams et. al., 2000a; Head, 2013; Studinski et al., 2006). For example, studies using the variable delay non-matching-to-position task (vDNMP), designed to assess cognitive aging in colony beagles, found that old age was related to an increase in the number of trials to acquisition and a decrease in spatial working memory (SWM) ability (Adams et al., 2000b; Head et al, 1995; Chan et al. 2002; Milgram et al., 1994; Studinski et al., 2006; Zanghi et al., 2015). Unfortunately, the vDNMP requires that the dog learn a conditional discrimination before undergoing the SWM test and is therefore limited in its ability to serve as a quick diagnostic tool (Piotti et al., 2017). A recent study implemented a visuo-spatial short-term memory task as a more efficient method to study canine aging and found that given as a one-time test, the task was proficient at separating the SWM abilities of young and old dogs (Piotti et al., 2017).

The SWM task that requires dogs to locate a hidden object after brief delays has been called the visible displacement task (VDT; Fiset et al., 2003), delayed-response task (Hunter, 1913), delayed-search task (Lazarowski et al., 2020), and working memory task (MacLean & Hare, 2018), among others, however, for the purpose of this paper we will refer to it as the VDT (Fiset et al., 2003). In all these tasks, a researcher hides a reward behind or inside of one of several stimulus positions while the dog watches. Then, following a varying delay interval, the dog is released to choose a stimulus position (e.g., Fiset et al., 2003). The longest delay at which the dog can successfully choose the stimulus position containing the reward is considered to reflect the dog's SWM ability. While this task was originally designed to evaluate object permanence and aspects of dogs' SWM (Gagnon & Doré, 1993), it has since gained popularity in other sectors, such as the study of aging mentioned above (Piotti et al., 2017; Van Bourg et al., 2020) and other applications. For example, recent studies have demonstrated the utility of SWM tasks as an efficient method for assessing and predicting working dog performance (Maclean & Hare, 2018; Lazarowski et al., 2020). With the benefits of the VDT becoming increasingly clear, evaluating the internal validity of the task (e.g., assessing non-mnemonic confounds) is critical.

A potential problem with using the VDT to study SWM is that non-mnemonic strategies, such as body cues or sustained attention, may be used to effectively solve the task. For example, if dogs use body cues such as orienting their head or body in the direction of the correct stimulus position for some or all of the delay interval, they may use these strategies to choose the correct stimulus position without relying on WM resources (Adams et al., 2000b). In addition, dogs could use sustained attention, or the ability to maintain focus on a specific stimulus or task, by visually fixating on the correct position during the delay interval (Chapagain et al., 2017). Some studies have applied a distraction technique, such as petting and talking to the dog during the delay interval, to eliminate these possible confounds (see Piotti et al., 2017 for an example). However, the potential effect of these distraction techniques on performance has not been assessed.

Other attempts have been made to control for the use of non-mnemonic strategies. For example, Fiset and colleagues (2003) implemented the use of a visual shield, placed directly between the dog and stimulus positions for the duration of the delay, to prevent the dog from visually fixating on the correct stimulus position. However, this method only accounts for the dog's ability to see the stimulus object, not the ability to remain visually fixated or with body orientation in its direction. Others sought to determine if the ability to use body cues or sustained attention affected VDT performance (Fiset et al., 2000, Gagnon & Doré, 1993, VanBourg et al., 2020). Fiset and colleagues (2000) found that head or body orientation during the delay did not affect VDT performance at 5 or 10 second delays, and Gagnon and Doré (1993) found that visual fixation to the correct stimulus position was disrupted periodically during 10- and 20- s delays and therefore could not account for VDT findings. Notably, however, physical orientation and visual fixation were not reported for the higher delays tested, leaving the possibility that dogs switch from WM to body cue or attentional resources as the task becomes more difficult. In addition, in these studies, orientation and visual fixation were coded as binary variables (i.e., the dog either did or did not orient for the entirety of the delay) which excludes the possibility that dogs use a combination of WM and non-mnemonic strategies by orienting or fixating periodically throughout the delay. Thus, it remains possible that performance on the VDT is confounded with non-mnemonic strategies and is not a valid measure of SWM.

Therefore, the goal of the current study was to explicitly control for the use of non-mnemonic strategies in the VDT by comparing performance on a VDT where body and attentional cues were available, to performance on a condition in which dogs were unable to orient or visually fixate to the correct position during the delay. We hypothesized that dogs would display lower performance in locating the displaced object when non-mnemonic strategies were controlled compared to the typical VDT, and that this effect would be explained by a positive relationship between orientation and performance. Previous studies that assessed the duration of dog SWM using the VDT found that dogs performed above chance for delays up to 240 seconds, therefore we predicted that dogs would remain above chance for the highest delay tested (90 seconds) on the regular study condition (Fiset et al., 2003). In contrast, we hypothesized that dogs would not remain above chance for the highest delay tested in the non-mnemonic control condition based on previous studies with dogs that found a steep decrease in performance between 60 and 90 seconds on delayed matching-to-sample tasks (Krichbaum et al., in press; Kuœmierek & Kowalska, 2002).

Methods

Subjects

Thirty-nine dogs (*Canis familiaris*) from the Auburn University Canine Performance Science breeding program were used in this study. The dogs were Labrador retrievers and varied in age (*M* = 3.31, min = 1.17, max = 6.75) and sex (Females = 19, Males = 20). Ethical approval was granted by the Auburn University Institutional Care and Use Committee (protocol #2020-3730).

Experimental setup

Sessions occurred in a building at the Canine Performance Sciences facility. The area consisted of two sections that were divided by movable plywood panels. The testing area (3.44 x 2.4 m) contained three 25.4 x 25.4 x 25.4 cm buckets placed open-end up, spaced 1 m apart and equidistant (2 m) to the center of the dog's start position. An additional (2.5 x 1 m) cardboard visual shield was positioned directly behind the buckets at the start of each trial during the regular study condition. The waiting area (2 x 2.2 m), outside of the test area, included a .5 x .5 m area designated the holding area (see Fig 1). The experimenter remained in the testing area and the handler remained in the waiting area for the duration of testing. A GoPro Hero 8 camera was used to record all sessions.

Task

General procedure. The VDT consisted of two conditions, one in which body and sustained attention strategies were possible (regular study), and one in which they were controlled (non-mnemonic control). Each condition began with warm-up trials in which dogs were required to reach an acquisition criterion with a one second delay. Once a dog met the acquisition criteria, they immediately advanced to delay testing. To control for order effects, the conditions were counterbalanced across dogs and there was a 30-minute break period between conditions. Directly following both conditions, dogs completed an odor control test to ensure that they were not relying on odor cues to solve the task.

Regular study condition. On each warm-up trial, the handler held the dog on a leash at the start position while the experimenter, located behind the visual shield, held up a toy (ChuckIt! ™*),* called the dog's name, and placed the ball inside of one of three buckets. The location of the ball (L, M, R) was counterbalanced across trials and the ball could not occur in the same bucket on more than two consecutive trials. Immediately after the experimenter placed the ball inside of one of the buckets, she moved the visual shield directly between the dog and the buckets for one second (Fig 1). This one second delay was imposed to match the inherent delay of the warm-up trials in the non-mnemonic control condition (see below). Following the one second delay, the experimenter moved the visual shield to the original spot behind the buckets and stood .5 m behind the middle bucket with her head down. The experimenter said “okay”, the handler released the dog, allowing 10 seconds for the dog to respond, defined as the dog’s nose coming within 5 cm of the opening of any bucket. A response to the correct bucket but not an incorrect bucket was reinforced by allowing the dog to retrieve the ball. Immediately following the initial response, the handler called the dog back to the waiting area. Upon a correct response, the hander handed the ball to the experimenter before she set up the next trial. If a dog took longer than 15 seconds to make a response, the dog was called back to the waiting area and the trial was noted as a time-out. If a dog had three time-outs during the warmup trials, they were excluded from participating in the study. The criteria to advance to delay testing was five out of six correct trials with a maximum of 24 trials. If a dog failed to meet the criteria in 24 trials, they were excluded from participating in delay testing.

Upon meeting the warm-up criteria, dogs began delay testing. Delay testing consisted of 12 trials that occurred the same as the warm-up trials but with four different delays (1, 30, 60, and 90 seconds) between when the experimenter placed the visual shield, which was in place for the entire delay interval, and when the dog was released. The delays were counterbalanced across testing such that each delay occurred three times, in random order. The visual shield remained in between the dog and the buckets for the duration of each delay. The experimenter timed the delay on a stopwatch and removed the visual shield following the delay, at which point the handler released the dog to make a choice.

Non-mnemonic control condition. The warm-up trials, with their criteria for advancing to delay testing of the non-mnemonic control condition, were the same as the regular study condition except after the experimenter placed the ball in one of the buckets, the handler moved the dog to the holding area for approximately one second. This one second delay was imposed to accustom the dog to moving to the holding area for delay testing. Delay testing consisted of 12 trials that occurred the same as the warm-up trials but with four different delays (1, 30, 60, and 90 seconds) between when the handler moved the dog to the holding area and when the dog was released. A visual shield was not used because the dogs were immediately moved to the holding area upon placement of the reward inside one of the buckets which controlled for the dog's ability to use non-mnemonic strategies to solve the task.

Odor control test. Following the experimental conditions dogs completed six odor control trials to assess their use of olfactory cues to solve the task. The trials were counterbalanced for position and the dog remained in the holding area while the experimenter placed the ball in one of the buckets. After the ball was placed, the experimenter returned to the start position, with her head down said "okay", and the dog was released to make a choice.

Scoring

An observer blind to the study hypotheses coded head and body orientation during the delay testing trials in the regular study condition using the latest version of Solomon Coder software (Péter, 2017). For each dog, total duration of head and body orientation towards the correct bucket were coded separately (9.05 minutes of total delay time). Orientation was coded as correct when the long axis of the dog's head or body was directed towards the correct bucket (Van Bourg et al., 2020).

Data analysis

We first conducted a generalized linear mixed-effects models (GLMM) with individual dog ID as a random factor to evaluate the effects of condition (regular study or non-mnemonic control) and condition order (1 or 2) on acquisition (# of trials to acquisition criteria) of the warm-up trials. Age and sex were added as additional fixed factors as well as all possible interactions. Next, we conducted a generalized linear mixed-effects model (GLMM) with a binomial family distribution (lme4 package; Bates et al., 2015) to assess percent correct during delay testing (correct: 1, incorrect: 0) as a function of condition (regular study or non-mnemonic control), delay (1, 30, 60, 90), condition order (1 or 2), trial number (1 to 12), sex, and age, with individual dog ID as a random factor, as well as all possible interactions. Dogs that performed two standard deviations below or above the mean on either condition were considered outliers and were removed from the analysis.

We also assessed average performance at each delay in both conditions to chance (33%) using a series of one-sample *t*-tests, with Bonferroni adjusted alphas ($p < .01$) to correct for multiple comparisons and compared average performance on one second delay trials between the conditions using a paired-sample *t*-test to ensure that the procedure in the non-mnemonic control condition was not creating distraction that influenced performance. We posited that if there was no significant difference in average performance between the conditions on one second delay trials and a significant interaction between delay and condition above, then any difference in performance between the conditions across longer delays could not be attributed to distraction caused by moving the dog to and from the holding area in the non-mnemonic control condition. In addition, we compared performance on odor control trials to chance (33%) using a one-sample *t*-test to ensure that dogs were not using odor cues to solve the task. Normality was assessed through visual inspection of the Q-Q plots.

To determine the extent that head and body orientation related to performance during delay testing in the regular study condition, we conducted Pearson correlations, with Bonferroni adjusted alphas ($p < .02$) to correct for multiple comparisons, between the percentage of delay (total delay time spent orienting / 9.05 minutes of total delay time) that the dog spent orienting their head or body toward the correct bucket and percent correct. Normality was assessed through visual inspection of Q-Q plots. In addition, Cronbach's test of reliability was conducted on 25% of the videos that were scored by a second independent coder to assess interrater reliability.

Results

Acquisition

There was a significant effect of condition on number of trials to warm-up criteria such that dogs took significantly more trials to acquire the task in the non-mnemonic control condition ($M = 10.82$, $SE = 1.15$) than the regular study condition ($M = 8.46$, $SE = .93$; GLMM: $z = 2.64$, $p = .012$). There were no significant effects of age, sex, or condition order and no significant interactions (ps > .11).

Delay testing

Five dogs were excluded from further analyses due to failure to meet the acquisition criteria on at least one of the conditions and one dog was excluded after being determined an outlier on the regular study condition. Figure 2 depicts average percent correct as a function of increasing delay during delay testing in the regular study and non-mnemonic control conditions. There was a significant effect of condition such that dogs performed better during delay testing in the regular study condition ($M = 77.78$, $SE = 2.63$) than the non-mnemonic control condition ($M = 66.92$, $SE = 2.45$; GLMM: $z = 3.55$, $p < .001$) and a significant decrease in performance across delays (GLMM: $z = -6.62$, $p < .001$). There was no interaction between condition and delay (GLMM: $z = .601$, $p = .55$), however, performance was equivalent at the one second delay in both conditions, $t(32) = 1.36$, $p = .18$. In addition, dogs remained above chance for delays up to 90 seconds on both conditions (*t*s > 4.31, *p*s < .001). There was a significant increase in performance across age (GLMM: $z = 2.21$, $p = .03$). However, there were no significant effects of sex, condition order, or trial number and there were no significant interactions (*p*s > .43).

Figure 3 depicts individual percent correct, collapsed across delays, as a function of the percentage of delay time that the dog spent orienting their head and body in the direction of the correct bucket during delay testing in the regular study condition. There were significant positive correlations between performance on the regular study condition and percentage of delay time spent orienting (head: $r(31) = .513$, $p = .002$, body: $r(31) = .447$, $p = .009$). Interrater reliability between scorers on the duration of head ($\alpha = .97$) and body ($\alpha = .97$) orientation was strong.

Odor control

Dogs did not perform significantly above chance on odor control trials ($M = 28.99$, $SE = 2.46$, $t(32) = -1.63$, $p = .12$).

Discussion

This study was the first to assess dogs' use of non-mnemonic strategies in the VDT by comparing performance on a condition in which dogs were able to orient or visually fixate to the correct position during the delay (regular study condition) to a controlled version when such strategies were removed (non-mnemonic control condition). Dogs required more trials to achieve the acquisition criteria in the non-mnemonic control compared to the regular study condition. As expected, dogs performed worse during delay testing in the non-mnemonic control condition compared to the regular study condition. Although there was no significant difference between the two conditions on one second delay performance, there was no interaction between delay and condition. Therefore, we are unable to rule out the possibility that performance during delay testing in the non-mnemonic control condition was influenced by distraction caused by moving the dog to and from the holding area. Additionally, dogs were not relying on odor cues to solve the task as dogs performed at chance levels on trials when the odor of the reward was the only cue available. These findings suggest that the non-mnemonic control condition better reflects the operation of a "purer" SWM process by eliminating the influence of non-mnemonic strategies (e.g., body cues or sustained attention). Previous studies implementing the VDT as a test of dog SWM were likely confounded with the use of such strategies due to allowing the dog to remain oriented in the direction of the correct stimulus position during the delays. Future work employing the VDT in dogs should consider the internal validity of the task and its implications for results.

An analysis of head and body orientation during delay testing in the regular study condition further supports our hypothesis that dogs rely on non-mnemonic strategies to solve the VDT. Dogs that spent a larger percentage of delay time orienting their head or body in the direction of the correct bucket performed better. Interestingly, this is the first study, since Hunter (1913), that suggests a strong relationship between orientation to the correct stimulus position and task performance in dogs. Hunter (1913) found that one dog was only correct on 12% of the delayed response trials in which his head was not oriented towards the correct position at the end of the delay. We propose that the conflicting results found in other studies using the VDT is due to the way orientation was coded (Fiset, 2000; Gagnon & Doré, 1993; VanBourg et al., 2020). In these cases, orientation was coded as a binary variable, which eliminates the possibility that orientation for a percentage but not all the delay facilitates performance. In fact, none of the dogs in the current study oriented their head (M = 39.71%, SE = 1.46) or body (M = 51.07%, SE = 2.27) for the entirety of the delay, suggesting that dogs use a combination of non-mnemonic strategies and SWM to solve the VDT task in the regular study condition. In other words, the partial use of non-mnemonic strategies elevates the memory function in the regular study condition requiring less time to maintain and remember the correct stimulus position in relation to the control condition (see Figure 2).

In line with past studies using the VDT in dogs, we found that performance on both conditions decreased with increasing delay. However, dogs remained above chance on the highest delay tested (90 seconds) in both conditions. Based on Fiset and colleagues (2003) finding that dogs could remember the position of a displaced stimulus for up to 240 seconds when not controlling for the use of non-mnemonic strategies, we thought it reasonable to predict that the dogs in the current study would remain above chance at 90 seconds in the regular study condition but that the forgetting function would appear steeper in the non-mnemonic control condition. In the absence of similar SWM tasks, our prediction of WM duration (assessed in the non-mnemonic control condition) was based on previous studies that implemented the matching-to-sample task to assess WM in dogs that found performance dropped to chance levels between 60 and 90 seconds for auditory (Kuœmierek & Kowalska, 2002) and odor stimuli (Krichbaum et al., in press). Although it was surprising that dogs remained above chance on delays up to 90 seconds in the non-mnemonic control condition, it is possible that the increased difficulty of a conditional discrimination or the lack of power due to small sample sizes in the previous matching-to-sample studies contributed to the shorter duration (8 and 5 dogs, respectfully). An important future direction of canine cognition is to systematically manipulate variables such as stimulus features, modality, and task difficulty to demonstrate how such variables impact memory (e.g., Wright, 2013).

Interestingly, we found that performance increased as a function of increasing age in both conditions. These results support previous work that used similar tasks to study the effects of canine development and aging (Chapagain et al., 2017; Piotti et al., 2017; Lazarowski et al., 2020; Van Bourg et al., 2020). For example, Van Bourg and colleagues (2020) found that performance on a staircase SWM task increased until approximately 84 months and Chapagain and colleagues (2017) found that performance on an attentional task increased with experience. As mentioned previously, short tasks to assess SWM in dogs have important applications to canine and human aging. However, additional research assessing performance on the controlled version of the VDT, across an evenly distributed age range, is necessary to draw conclusions regarding the mechanisms responsible for the apparent functions.

Conclusion

This study reports the first evidence that controlling for the use of non-mnemonic strategies negatively affects dogs' performance on a task purported to measure SWM. We found VDT performance was lower when the use of body cues and sustained attention were experimentally controlled suggesting that the non-mnemonic control condition was more "purely" assessing SWM rather than the ability to use non-mnemonic strategies. Although we recognize the value of previous VDT results on applied avenues such as canine aging and individual differences, we urge the field to recognize the internal validity of the VDT if used to explicitly measure SWM moving forward. Future studies should aim to replicate previous findings on SWM in relation to aging and individual differences using a version of the VDT that controls for non-mnemonic strategies, to determine whether previous results can be attributed to SWM or other processes.

References

Adams, B., Chan, A., Callahan, H., & Milgram, N. W. (2000a). The canine as a model of human cognitive aging: recent developments. *Progress in Neuro-Psychopharmacology and Biological Psychiatry*, *24*(5), 675-692. https://doi.org/10.1016/s0278-5846(00)00101-9

Adams, B., Chan, A., Callahan, H., Siwak, C., Tapp, D., Ikeda-Douglas, C., ... & Milgram, N. W. (2000b). Use of a delayed non-matching to position task to model age-dependent cognitive decline in the dog. *Behavioural Brain Research*, *108*(1), 47-56. https://doi.org/10.1016/S0166-4328(99)00132-1

Baddeley, A. D. (2017). The concept of working memory: A view of its current state and probable future development. In *Exploring Working Memory* (pp. 99–106). London, U.K.: Routledge.

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software*, *67*(1), 1–48. https://doi.org/10.18637/jss.v067.i01

Bensky, M. K., Gosling, S. D., & Sinn, D. L. (2013). The world from a dog's point of view: a review and synthesis of dog cognition research. In *Advances in the Study of Behavior* (Vol. 45, pp. 209-406). Academic Press.

Chan, A. D. F., Nippak, P. M. D., Murphey, H., Ikeda-Douglas, C. J., Muggenburg, B., Head, E., Cotman, C. W., & Milgram, N. W. (2002). Visuospatial impairments in aged canines (*Canis familiaris*): The role of cognitive-behavioral flexibility. *Behavioral Neuroscience*, *116*(3), 443–454. https://doi.org/10.1037/0735-7044.116.3.443

Chapagain, D., Virányi, Z., Wallis, L. J., Huber, L., Serra, J., & Range, F. (2017). Aging of attentiveness in border collies and other pet dog breeds: the protective benefits of lifelong training. *Frontiers in Aging Neuroscience*, *9*, 100. https://doi.org/10.3389/fnagi.2017.00100

Fiset, S., Beaulieu, C., & Landry, F. (2003). Duration of dogs' (*Canis familiaris*) working memory in search for disappearing objects. *Animal Cognition*, *6*(1), 1-10. https://doi.org/10.1007/s10071-002-0157-4

Fiset, S., Gagnon, S., & Beaulieu, C. (2000). Spatial encoding of hidden objects in dogs (Canis familiaris). *Journal of Comparative Psychology*, *114*(4), 315. https://doi.org/10.1037/0735-7036.114.4.315

Gagnon, S., & Doré, F. Y. (1993). Search behavior of dogs (*Canis familiaris*) in invisible displacement problems. *Animal Learning & Behavior*, *21*(3), 246-254. https://doi.org/10.3758/BF03197989

Head, E., Mehta, R., Hartley, J., Kameka, M., Cummings, B. J., Cotman, C. W., ... & Milgram, N. W. (1995). Spatial learning and memory as a function of age in the dog. *Behavioral Neuroscience*, *109*(5), 851. https://doi.org/10.1037/0735-7044.109.5.851

Head, E. (2013). A canine model of human aging and Alzheimer's disease. *Biochimica et Biophysica Acta (BBA)-Molecular Basis of Disease*, *1832*(9), 1384-1389. https://doi.org/10.1016/j.bbadis.2013.03.016

Honig, W. K. (1978). Studies of working memory in the pigeon. *Cognitive Processes in Animal Behavior*, *211*, 248.

Hunter, W. S. (1913). The delayed reaction in animals and children. *Behavior Monograhs*, *2*, 1-85.

Krichbaum, S., Lazarowski, L., Davila, A., Cox, E., Smith G. J., Waggoner L. P., Katz, J. (2021). Dissociating the effects of delay and interference on dog (*Canis familiaris*) working memory. *Animal Cognition.* https://doi.org/10.1007/s10071-021-01509-0

Kuœmierek, P., & Kowalska, D. M. (2002). Effect of sound source position on learning and performance of auditory delayed matching-to-sample task in dogs. *Acta Neurobiologiae Experimentalis*, *62*(4), 251-262.

Lazarowski, L., Krichbaum, S., Waggoner, L. P., & Katz, J. S. (2020). The development of problem-solving abilities in a population of candidate detection dogs (*Canis familiari*s), *Animal Cognition*, 23(4), 755-768. https://doi.org/10.1007/s10071-020-01387-y

MacLean, E. L., & Hare, B. (2018). Enhanced selection of assistance and explosive detection dogs using cognitive measures. *Frontiers in Veterinary Science*, *5*, 236. https://doi.org/10.3389/fvets.2018.00236

Miklósi, Á. (2015). *Dog behaviour, evolution, and cognition* (2nd ed.). Oxford University Press. https://doi.org/10.3389/fvets.2018.00236

Milgram, N. W., Head, E., Weiner, E., & Thomas, E. (1994). Cognitive functions and aging in the dog: acquisition of nonspatial visual tasks. *Behavioral Neuroscience*, *108*(1), 57. https://doi.org/10.1037//0735-7044.108.1.57

Olsen, M. R. (2018). A case for methodological overhaul and increased study of executive function in the domestic dog (*Canis lupus familiaris*). *Animal Cognition*, *21*(2), 175-195. https://doi.org/10.1007/s10071-018-1162-6

Olton, D. S., & Samuelson, R. J. (1976). Remembrance of places passed: spatial memory in rats. *Journal of Experimental Psychology: Animal Behavior Processes*, *2*(2), 97. https://doi.org/10.1037/0097-7403.2.2.97

Péter, A. (2017). Solomon coder. *Version beta*, *17*, 22.

Piotti, P., Szabó, D., Wallis, L., Bognár, Z., Stiegmann, B., Egerer, A., ... & Kubinyi, E. (2017). The effect of age on visuo-spatial short-term memory in family dogs. *Pet Behaviour Science, 4*, 17-19. https://doi.org/10.21071/pbs.v0i4.10130

Shettleworth, S. J. (2009). *Cognition, evolution, and behavior*. Oxford University Press.

Studzinski, C. M., Christie, L. A., Araujo, J. A., Burnham, W. M., Head, E., Cotman, C. W., & Milgram, N. W. (2006). Visuospatial function in the beagle dog: an early marker of cognitive decline in a model of human aging and dementia. *Neurobiology of Learning and Memory*, *86*(2), 197-204. https://doi.org/10.1016/j.nlm.2006.02.005

Van Bourg, J., Gilchrist, R., & Wynne, C. D. (2020). Adaptive spatial working memory assessments for aging pet dogs. *Animal Cognition*, 1-21. https://doi.org/10.1007/s10071-020-01447-3

Wright, A. A. (2013). Functional relationships for investigating cognitive processes. *Behavioural Processes*, *93*, 4-24. https://doi.org/10.1016/j.beproc.2012.11.003

Zanghi, B. M., Araujo, J., & Milgram, N. W. (2015). Cognitive domains in the dog: independence of working memory from object learning, selective attention, and motor learning. *Animal Cognition*, *18*(3), 789-800. https://doi.org/10.1007/s10071-015-0847-3

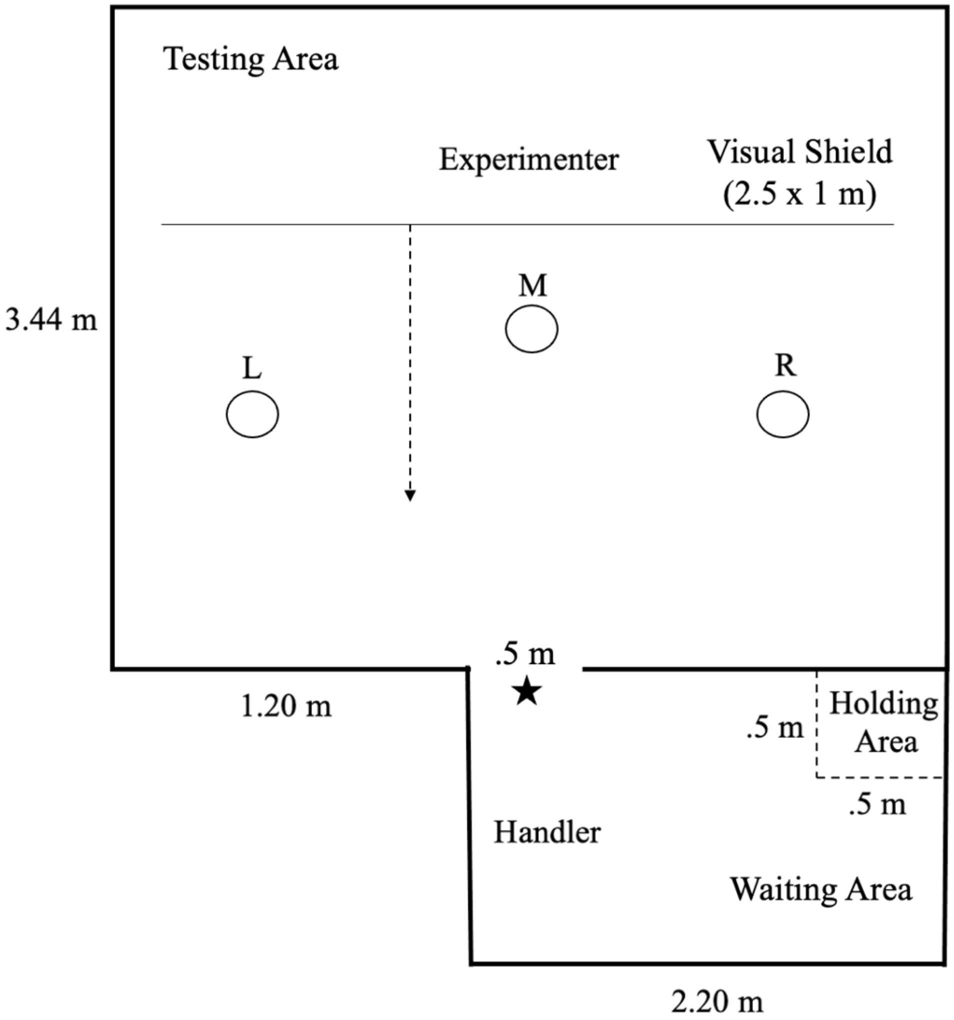


Figure 1. Schematic representation of the experimental area (not drawn to scale). During delay testing in the regular study condition, the experimenter, held up a ball, called the dog's name (located at the start position represented by the star), and placed the ball inside of one of buckets. Immediately after the experimenter placed the ball inside of one of the buckets, she moved the visual shield directly between the dog and the buckets for the designated delay. Following the delay, the experimenter moved the visual shield to the original location behind the buckets for the duration of the delay. Delay testing in the non-mnemonic control condition occurred the same as delay testing in the regular study condition, except the dog was moved to the holding area for the duration of the delay and the visual shield was not present.

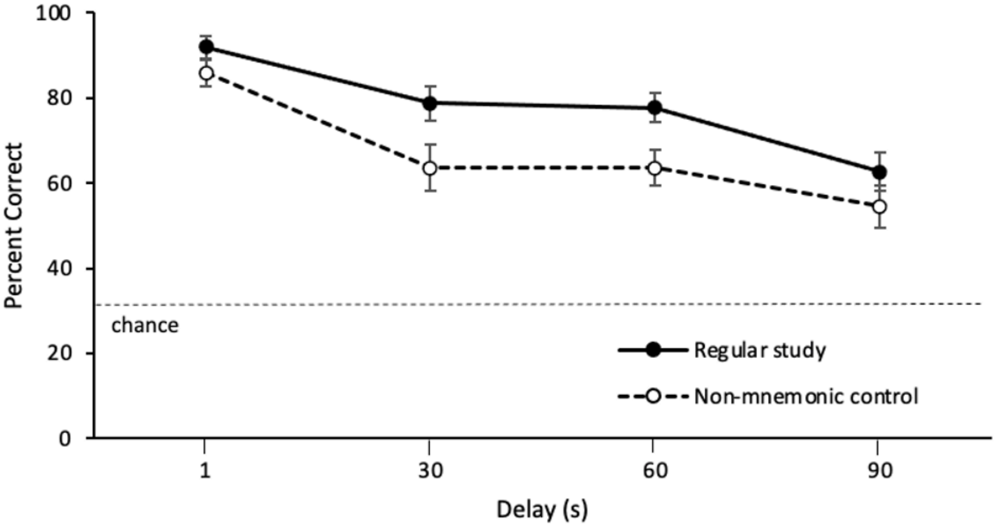


Figure 2. Average percent correct as a function of increasing delay during delay testing in the regular study and non-mnemonic control conditions. Error bars are standard errors of the mean. Dotted line represents chance (33.33%).

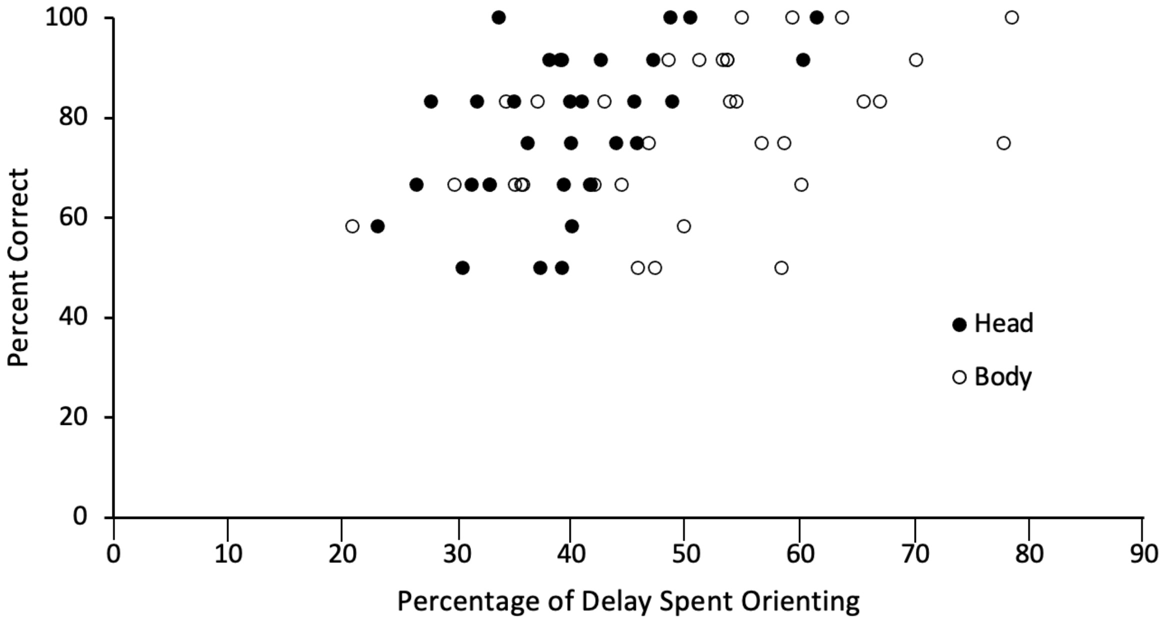


Figure 3. Individual percent correct, collapsed across delays, as a function of the percentage of time the dog spent orienting their head and body in the direction of the correct bucket during delay testing in the regular study condition.

Chapter 4: Spatial Discounting Test to Assess Inhibitory Control in Dogs: Relationships to Executive Function Tasks and Detection Dog Suitability

Abstract

The implementation of single session cognitive tasks to assess inhibitory control and other executive functions in dogs are useful in several domains (e.g., predicting working dog suitability). However, they often display poor validity evidenced by a lack of cross-task correlations. The current study assessed the validity of the Spatial Discounting Test (SDT) as a measure of inhibitory control in dogs and found that it did not relate to another a task assessing inhibitory control (Cylinder Task) but did relate to a task assessing working memory (Visible Displacement Task; VDT). The lack of relationship between tasks purported to examine inhibitory control is discussed in terms of motivational factors that can influence performance (e.g., arousal) and the correlation between the SDT and VDT is the first evidence of a relationship between tasks purported to measure working memory and inhibitory control in dogs. Executive function task performance was also related to two domains of detection dog suitability: performance and environmental soundness. Performance on the Cylinder Task negatively related to detection dog performance and environmental soundness while performance on the SDT and VDT positively related to environmental soundness. We believe these findings support the cross-task relationships which suggest that the Cylinder Task and SDT are measuring distinct constructs. For example, results from the Cylinder Task can be explained by the propensity to select dogs with certain motivational traits (i.e., those that display high work arousal), while the results from the SDT and VDT imply that detection dogs possess and rely on executive functions to be successful in their work.

Keywords: inhibitory control, executive functions, detection dogs

Introduction

Inhibitory control (IC) is an executive function that allows an organism to inhibit an impulsive response, typically for a smaller or sooner reward, for a more advantageous response, typically for a larger or later reward (Beran, 2015). While IC has been widely studied in humans (Diamond, 2013) and other animals (Beran, 2015) there are many benefits of examining IC in dogs (Arden et al., 2016; Olson, 2018; Troisi et al., 2019). First, a better understanding of how IC is affected by factors such as age (Tapp et al., 2003) and life history (Fagnani et al., 2016) will allow stakeholders (e.g., owners, researchers, veterinarians) to understand how to properly care for specific groups of dogs. Second, due to the close link between self-control and intelligence (Beran, 2015), as well as the increased effort to identify cognitive factors that relate to working dog suitability, it remains necessary to explore if measures of IC can be used to predict working dog success (Troisi et al., 2019).

Researchers have implemented a wide variety of tasks to uncover novel findings regarding IC in dogs (see Olson, 2018 for a review). These studies have examined increases across development (Bray et al., 2014; Lazarowski et al., 2020a) and decreases across old age (Mongillo et al., 2013; Piotti et al., 2018a; Tapp et al., 2003). They also discovered the effects of training (Barrera et al., 2019), domestication (Marshall-Picini et al., 2015), life history (Fagnani et al., 2016), and arousal on IC (Bray et al., 2015) as well as the relationship between IC and suitability in guide dogs (Bray et al., 2014), sled dogs (Kelly et al., 2019), and detection dogs (Brady et al., 2018a; Lazarowski et al., 2020a; Maclean & Hare, 2018; Tiira, 2020). While these results have direct benefits to dog welfare, training, and working dog programs, there is poor construct validity represented by the lack of correlations between the current measures of IC

(Bray et al., 2014, Brucks et al., 2017; Fagnani et al., 2016; Vernoullit et al., 2018) that needs to be addressed before concluding that IC is responsible for past findings.

Due to increasing evidence that measures of IC and other executive functions (e.g., working memory) can predict detection dog success (Brady et al., 2018a; Maclean & Hare et al., 2018; Lazarowski et al., 2020a; Tiira et al., 2020), as well as the increasing demand for detection dogs (Lazarowski et al., 2020b; Leighton et al., 2018; Otto et al., 2019), it remains imperative to distinguish the link between executive functions and detection dog suitability. Lazarowski et al. (2018) and Lazarowski (2021a) outline two major domains of detection dog work, performance and environmental soundness, that may be related to executive function abilities. Detection dog performance encompasses all the characteristics related to successful search behavior (e.g., motivation to hunt for targets for extended periods of time) and there is evidence that these characteristics relate to tasks purported to measure executive functions (Brady et al., 2018a; Bray et al., 2014; Maclean & Hare et al., 2018; Lazarowski et al., 2020a; Tiira et al., 2020). However, there are conflicting findings amongst studies. For example, Tiira and colleagues (2020) found that dogs that displayed better IC on the cylinder task (in which a dog must inhibit running in to a transparent cylinder to retrieve a ball from the opening in the side) found more explosives in an area search task, while others found no relationship between performance on the cylinder task and detection dog success (Maclean & Hare, 2018; Lazarowski et al., 2020a). This may be due to differences in the way these groups define suitability or differences in the populations tested. Additional research is necessary to determine the strength and direction of the relationships between executive functions and detection dog work.

Environmental soundness or dogs' ability to adapt to and react appropriately to potential stressors (Lazarowski et al., 2018, Lazarowski et al., 2020b, Lazarowski et al., 2021) is another domain that may have a direct link to IC and other executive functions. Environmental soundness is often measured in terms of emotional reactivity or the intensity of all responses to novel stimuli (Scott and Fuller, 1965). For example, an emotional reactivity test in dogs that involved scoring their reactions to several distinct novel or startling stimuli found that lower levels of emotional reactivity were predictive of detection dog success as early as three months of age (Lazarowski et al., 2021a). Therefore, it is reasonable to expect that executive functions, which are needed to perform goal-directed (e.g., resisting impulsive actions) versus automatic reactions (e.g., acting impulsively; Foraita et al., 2021), may be related to emotional reactivity in these assessments (Diamond et al., 2013). Despite this apparent link, research on the relationship between executive functions and emotional reactivity in dogs is surprisingly lacking.

The current study implemented the recently developed, Spatial Discounting Test (SDT) task to measure IC in dogs (Brady et al., 2018b). The SDT is an IC task in which a dog is required to inhibit choosing a closer reward of a lower value or quantity to choose a reward of higher value or quantity that is farther away. In other words, the dog is required to travel past the low value reward to arrive at the high value reward, encouraging the dog to inhibit a prepotent response to the low value reward. The purpose of employing this task is two-fold. First, it will allow the opportunity to assess the construct validity of the SDT by correlating performance with tasks that are commonly used to assess IC (Cylinder Task) and other measures of executive function (sustained attention and working memory in the Visible Displacement Task; VDT), while ruling out similar constructs, such as persistence (Unsolvable Task). Second, the relationship among all tasks purported to assess executive functions and detection dog suitability will be determined. We hypothesize that SDT performance will not correlate with other measures of IC and executive functions providing additional evidence of the poor construct validity amongst tasks purported to assess IC in dogs (Bray, Maclean, & Hare, 2014, Brucks et al., 2017; Fagnani et al., 2016; Vernoullit et al., 2018). In addition, we hypothesize that performance on the Cylinder Task will negatively correlate to measures of detection dog suitability in two domains: detection performance (Brady et al., 2018; Bray et al., 2015; Maclean & Hare, 2018; Lazarowski et al., 2020a; Tiira et al., 2020) and environmental soundness (Foraita et al., 2021) based on previous findings that dogs with higher arousal are more likely to be selected for detection work and are less likely to perform well on the Cylinder Task. In contrast we hypothesize that performance on the SDT and VDT will correlate positively based on previous studies that found similar relationships between the VDT and detection dog performace. These relationships will be assessed with a trainer survey on detection dog performance characteristics (Rooney et al., 2007) and an internal program assessment called the emotional reactivity test (ERT; Lazarowski et al., 2021a), respectively.

Methods

Subjects

42 purpose-bred detection dogs (*Canis familiaris*) from the Auburn University Canine Performance Science Program were used in this study. The minimum number of dogs required was determined by an a priori power analysis with a desired effect size (f^2) of .15 and a desired power of .8 with an alpha of .05 (Gpower: Erdfelder & Faul, 1996). The dogs were Labrador retrievers and varied in age (*M* = 5.91, min = 1.22, max = 7.69) and sex (Females = 19, Males = 23). Ethical approval was granted by the Auburn University Institutional Care and Use Committee (protocol #2020-3730).

Apparatus

Test sessions occurred in a building at the Canine Performance Science center. The area consisted of two sections (test area and holding area) that were divided by movable plywood panels (see Figure 1). The test area consisted of two lanes (each 9 m x 2 m). The start point was in the center of the opening between the holding and test areas (1 m). Plastic stimulus carts (40.64 x 40.64 x 35.56 cm) on wheels were placed 25 cm on either side of the 9 x 1 m wall separating the two lanes and 2 m away from the start point. The experimenter remained outside of the test area and the handler remained in the holding area while the dog was inside the test area as to not influence the dog's choice. A GoPro Hero 8 camera was used to record all sessions.

General procedure

Dogs completed the SDT task which included preference and inhibitory control tests adapted from Brady et al. (2018b) as well as the Cylinder (Bray et al., 2014) and Unsolvable (Passalacque et al., 2011) Tasks. A portion of the dogs in this study also completed two conditions of the VDT (Non-Mnemonic Control and Regular Study; Krichbaum et al., in press). All tasks occurred at the same time of day (8-10 am). In addition, the dog's primary trainers filled out a survey that consisted of a validated scale representing individual dogs' performance characteristics related to odor detection (Rooney et al., 2007). Trainers were required to work with the dog for a minimum of one month before filling out the survey. All dogs also completed an internal emotional reactivity assessment to assess their environmental soundness.

Spatial Discounting Test

A priori motivation test. To begin, a treat (BilJac PBnanas®) was placed on a stimulus cart one side of the wall separating the two lanes and 2 m away from the start point. The handler escorted the dog to the start point and released the dog to make a choice. The amount of time (s) that the dog took to choose the treat (consuming the treat) was recorded. Following the trial, the dog was moved to the holding area while the experimenter set up an identical trial with the ball (ChuckIt®) on the opposite side of the wall. Again, the amount of time (s) that the dog took to choose the ball (pick up the ball) was recorded. Dogs that took longer than 15 seconds to choose either reward were excluded from participating in the rest of the study.

Preference test. Dogs first underwent a two-choice preference test between a treat and ball to determine their high- (HVR) and low-value rewards (LVR). The items were placed on stimulus carts that remained on either side of the wall separating the two lanes and 2 m away from the start point (see Figure 1A). On every trial, the handler escorted the dog to the start point and released the dog to make a choice. Upon choosing either the treat (consuming the treat) or ball (touching the ball), the dog was moved to the holding area while the experimenter set up the next trial. Trials were repeated until the dog chose one of the rewards on 9/12 consecutive trials. The preferred reward was deemed the HVR, and the other was deemed the LVR for subsequent testing. Dogs that did not meet preference criteria in 24 consecutive trials were excluded from participating in the rest of the study.

Inhibitory control test. Following the preference test, we evaluated dogs' inhibitory control using an adapted version of the SDT task (see Brady et al., 2018b) in which a dog is required to inhibit choosing a closer reward of a lower value or quantity to choose a reward of higher value or quantity that is farther away. In this test, inhibitory control was measured by the maximum distance a dog would travel (MDT) to choose their HVR, without responding to the closer LVR. For instance, on trial 1 (Figure 1B), the stimulus cart containing the LVR remained in its original position (25 cm away from the middle wall and 2 m away from the start point), while the stimulus cart containing the HVR was moved to level 1 (25 cm behind its original position). The handler escorted the dog to the start point and released the dog to make a choice. Upon choosing either the HVR or LVR, the dog was moved to the holding area while the experimenter set up the next trial. If the dog chose the HVR then the experimenter moved the stimulus cart containing the HVR to level two (25 cm behind level 1) and the rewards were replenished, but if the dog chose the LVR, the carts remained in position and the rewards were replenished. The task continued in this manner until the dog chose the LVR on four consecutive trials. At this point the test ended and the primary dependent variable, MDT, was recorded as the highest level the stimulus cart containing the HVR reached. In addition to MDT, First Switch, or the level at which the stimulus cart containing the HVR was placed on the trial in which the dog first chose the LVR, was recorded.

Motivation control. To determine if a decrease in motivation or fatigue was the cause of the switch from the HVR to the LVR, dogs completed a motivation control trial directly after the IC test. The stimulus carts containing both the HVR and the LVR were placed on either side of the wall separating the lanes at the very last level (36) of the IC test. As in previous trials, the handler escorted the dog to the start point and released the dog to make a choice between the HVR and LVR. We hypothesized that if the switch was due to due a lack of inhibitory control, the dog would choose the HVR on this trial. The results for this task were analyzed with and without dogs that chose the LVR on this trial.

Run control. An additional control trial was used to determine if dogs' willingness to travel distances for the HVR was due to dogs finding running itself rewarding (Brené et al., 2007). On this trial, the stimulus cart containing the HVR was placed at the first level (1) while the stimulus cart containing the LVR was placed at the very last level (36). We hypothesized that if the dog's willingness to travel distance for their HVR was due to the rewarding nature of running rather than IC then the dog would choose their LVR on this trial. Therefore, dogs that choose the LVR on this trial were excluded from the data analysis.

Cylinder Task

In addition to the SDT, dogs also completed the Cylinder Task (adapted Bray et al., 2014) to determine the relationship between two tasks purported to assess IC. Based on previous findings that reward value and type (ball or treat) influence performance on the Cylinder Task (Lazarowski & Krichbaum, 2021b), we used the results from the preference test to conduct the Cylinder Task with the dogs' HVR.

In the Cylinder Task, a clear plastic cylinder (25 cm x 25 cm) was attached to a wooden base and placed 2 m in front of the dog. First, the dogs completed warm-up trials in which the cylinder was made opaque by attaching a laminated sheet to the outside. On these trials the experimenter, standing directly behind the cylinder, held up the dogs LVR, called the dog's name and placed the reward in the center of the cylinder through the opening on the dogs left. Immediately after the reward was placed, the handler released the dog, allowing 15 seconds to retrieve the reward. If the dog retrieved the reward without touching the exterior of the cylinder the trial was marked correct whereas if at any point the dog's nose or paws touched the exterior of the cylinder the trial was marked incorrect. If the dog failed to retrieve the reward within 15 seconds the trial was marked as a time-out and repeated. Upon completing one correct trial, the dog began the cylinder test.

The cylinder test consisted of 10 trials that were conducted the same as warm-up trials except the laminated sheet was removed so that the reward could be seen through the clear plastic. The primary dependent measure was Overall Percent Correct calculated as the number of correct trials divided by the total number of trials.

Unsolvable Task

The dogs were tested on the Unsolvable Task (adapted from Passalacque et al., 2011) to examine the relationship between persistence and SDT performance (Van Horik et al., 2019). In this task, the lid of a 11 x 14 x 14-cm transparent container (Sterilite®), was drilled to a 45-cm wood on board (Lazarowski et al., 2019). Depending on the trial type, the container, containing the dogs HVR (treat or ball) was either insecurely (solvable trials) or securely (unsolvable trials) attached to the lid. The task began with three solvable trials in which the handler escorted the dog to the start point (1 m in front of the container) and released the dog to retrieve the HVR. The trial ended when the dog successfully opened the container (with their paw or mouth) and retrieved the ball. Following the solvable trials, the dog completed one unsolvable trial. Again, the dog was brought to the start point and released. The dog was allotted 60 seconds to attempt to retrieve the HVR. The primary dependent measure recorded during the 60 seconds of the unsolvable trial was the duration of persistent behavior, defined as physical contact with the apparatus.

Visible Displacement Task

Apparatus. The area consisted of two sections that were divided by movable plywood panels. The testing area (3.44 x 2.4 m) contained three 25.4 x 25.4 x 25.4 cm buckets placed open-end up, spaced 1 m apart and equidistant (2 m) to the center of the dog's start position.

Procedure. A portion of the dogs tested on the SDT (n = 31) completed two conditions (Regular Study and Non-Mnemonic Control) of the VDT (Krichbaum et al., in press). Each condition began with warm-up trials in which the handler held the dog on a leash at the start position while the experimenter held up a ball, called the dog's name, and placed the ball inside of one of three buckets. Immediately after, the dog either remained at the start position (in view of the stimulus positions) in the Regular Study condition or was moved by the handler to a holding area, away from the start position, for one second so that the dog was unable to use non-mnemonic cues such as orienting towards the correct stimulus position to solve the task in the Non-Mnemonic Control condition. The experimenter said “okay”, the handler released the dog, allowing 10 seconds for the dog to respond, defined as the dog’s nose coming within 5 cm of the opening of any bucket. A response to the correct bucket but not an incorrect bucket was reinforced by allowing the dog to retrieve the ball. The criteria to advance to delay testing was five out of six correct trials with a maximum of 24 trials. If a dog failed to meet the criteria in 24 trials, they were excluded from participating in delay testing. Delay testing consisted of 12 trials that occurred the same as the warm-up trials but with four different delays (1, 30, 60, and 90 seconds) between when either the dog remained at the start position (in view of the stimulus positions) in the Regular Study condition or was moved by the handler to a holding area in the Non-Mnemonic Control Condition and when the dog was released. The primary dependent variables from this task were Number of Trials to Warm-Up Criteria and Overall Percent Correct in delay testing.

Detection dog suitability

Performance. To examine the relationship performance on the SDT, Cylinder task, VDT, and desirable detection dog traits, trainers filled out a validated 12-question survey, originally designed to evaluate performance in search dogs, to evaluate each dog on various performance characteristics that are considered desirable attributes of detection dogs (Rooney et al., 2007). The items included: Obedience to Human Commands, Boldness, Playfulness, Tendency to Hunt by Smell Alone, Stamina, Ability to Learn by being Rewarded, Interest in Toys or Objects, Acuity of Sense of Smell, Motivation to Retain Possession of an Object, and Overall Ability. The dogs were rated on the level to which they display that characteristic on a 5-point Likert scale (1: extremely low, 5: extremely high) and a mean Overall Suitability Score was calculated for each dog such that higher scores represented more desirable detection performance characteristics. Trainers were required to work with the dog for a minimum of one month prior to filling out the survey.

Environmental soundness. Executive function task performance was compared to dogs' scores on an ERT (e.g., Lazarowski et al., 2021a). The ERT is a standardized behavioral assessment in which dogs encounter several novel or surprising stimuli (e.g., dinosaur statue, animated toys), in this case five stimuli were used. Reactions to and recovery from each stimulus were coded using validated guidelines for working dogs (International Working Dog Registry, 2021) on a Likert-type scale (1 = "severe concern or fear reaction" to 5 = "no startle response"; Lazarowski et al., 2021a). Following completion of the test, the scores were aggregated to create a final ERT Score such that higher scores represented lower emotional reactivity behavior (higher environmental soundness).

Data analysis

We determined and transformed outliers using a 90 percent winsorization for First Switch and MDT in the SDT. Then we conducted generalized linear models (GLMs) to evaluate the effect of strength of preference, HVR type, age, and sex as well as their interactions on First Switch and MDT, with and without dogs that chose their LVR on the motivation control trial. To further assess the validity of the SDT as a task to measure IC and executive functioning in dogs, we also conducted Spearman correlations between First Switch and MDT in the SDT, Overall Percent Correct in the Cylinder Task, and Number of Trials to Warm-Up Criteria as well as Overall Percent Correct on delay testing on the Regular Study and Non-Mnemonic Control conditions in the VDT. Due to previous research suggesting that reward preference and type can influence cognitive task performance (Lazarowski & Krichbaum, 2021b), the cross-task correlations were split between dogs that preferred the ball versus the treat and all tasks were conducted with the dogs HVR, except for the VDT which was conducted prior to this study in a subset of dogs and used the ball only. Therefore, only dogs that preferred the ball in the Preference Test were used in analyses with the VDT. We also conducted Spearman correlations, separated by HVR reward type, between First Switch and MDT in the SDT to the duration of time spent in physical contact with the apparatus in the Unsolvable Task to rule out First Switch and MDT as measures of persistence.

To elucidate the relationship between SDT as well as other executive function tasks and desirable performance characteristics in detection dogs we conducted Spearman correlations between executive function task measures and Overall Suitability Scores derived from the trainer survey (Rooney et al., 2007). In addition, to assess the relationship between executive function tasks and environmental soundness in detection dogs we conducted Spearman correlations between executive function task measures and ERT Scores separated by HVR type. Normality of all correlations were assessed through visual inspection of the Q-Q plots and Bonferroni correction was not used because all of tests had predetermined hypotheses (Armstrong, 2014; Perneger, 1998).

Results

Spatial Discounting Test

All dogs consumed the treat or picked up the ball within 15 seconds in the apriori motivation test. However, three dogs did not meet the preference criteria of 9/12 consecutive choices to a single reward type within 24 trials in the preference test and were excluded from participating in the rest of the study. Of the remaining dogs, 16 preferred the treat and 23 dogs preferred the ball reward and met the preference test criteria in significantly fewer trials (*M* = 11.28, *SEM* = 4.89) than the maximum allotted (*t*(38) = -26.03, *p* < .001). A 90 percent winsorization revealed no outliers in the IC test for either dependent variable (First Switch or MDT). In addition, generalized linear models revealed that First Switch and MDT of the inhibitory control test were not significantly affected by strength of preference, HVR type, age or sex and there were no interactions (First Switch level: *M* = 12.74, *SEM* = 2.17, *t*s < 1.31, *p*s > .16; MDT: *M* = 22.03, *SEM* = 2.3, *t*s < .91, *p*s > .21) suggesting that they may be valid assessments of IC. Following the IC test, five dogs chose their LVR on the motivation control trial, therefore, the linear models were repeated with those dogs removed. There were still no effects of strength of preference, HVR type, age or sex and no interactions on First Switch (*t*s < 1.53, *p*s > .14) or MDT (*t*s < 1.23, *p*s > .23), therefore, those five dogs were included in the following results. In addition, all dogs that completed the run control trial (n = 23) chose their LVR which suggests that running as a reward did not influence performance in the IC test.

Spatial Discounting Test and Unsolvable Task

There were no significant correlations between First Switch or MDT in the SDT and percentage of time spent in physical contact with the apparatus in the Unsolvable Task with dogs that preferred the treat (*p* = ns) or ball (*p* = ns) ruling out the possibility that SDT was assessing reward persistence instead of IC.

Executive function tasks

The results of Spearman correlations, separated by HVR type, to assess the validity of the SDT as a measure of executive functioning in dogs are shown in Table 1 (HVR: ball) and 2 (HVR: treat). In dogs that preferred the ball, there was a significant positive correlation between

First Switch and MDT in the SDT (*r*(21) = .771, *p* < .001) and a significant negative correlation between First Switch in the SDT and number of trials to warm-up criteria on the non-mnemonic control condition in the VDT (*r*(15) = -.592, *p* = .012; Figure 2). In dogs that preferred the treat, there was a positive correlation between First Switch and MDT in the SDT (*r*(14) = .785, *p* < .001). All other correlations were non-significant (*p*s = ns).

Executive functions and detection dog suitability

Spearman correlations, separated by HVR type, to elucidate the relationship between executive functions and desirable performance characteristics in detection dogs assessed by the trainer survey (Rooney et al., 2007) are outlined in Tables 3 (HVR: ball) and 4 (HVR: treat). Figure 3 shows that in dogs that preferred the treat there was a significant negative correlation between Overall Percent Correct in the Cylinder Task and Overall Suitability Score (*r*(14) = -.609, *p* = .012). All other correlations were non-significant (*p*s = ns).

To assess the relationship between executive functions and environmental soundness additional Spearman correlations, separated by HVR type, between executive function task performance and the ERT Score were conducted. In dogs that preferred the ball there was a significant positive correlation between First Switch in the SDT and ERT Score (*r*(21) = .514, *p* = .012; Figure 4) and significant negative correlation between number of trials to criteria on the non-mnemonic control condition in the VDT and ERT Score (*r*(15) = -.625, *p* = .007; Figure 5). In dogs that preferred the treat there was a significant negative correlation between overall percent correct in the Cylinder Task and ERT Score (*r*(13) = -.637, *p* = .001; Figure 6). All other correlations were non-significant (*p*s = ns).

Discussion

We assessed the validity of the, recently developed, SDT task (Brady et al., 2018b) as a measure of IC in dogs and found that performance on the task was not influenced by strength of preference, HVR type, age, or sex. In addition, individual differences in reward motivation (i.e., a priori motivation test), post-test reward motivation (i.e., motivation control trial), and the reward of running (i.e., run control trial), did not affect SDT performance. Cross-task correlations between SDT (First Switch and MDT) and the Unsolvable Task (i.e., percentage of time spent in physical contact with the apparatus) revealed no relationships in dogs that preferred the ball or treat. Taken together, these results suggest that the SDT is capturing a mechanism that is partially separate from general reward motivation and persistence.

Correlations between tasks purported to measure executive functions in dogs (including the SDT, Cylinder Task, and two conditions of the VDT) revealed a significant negative correlation between First Switch in the SDT and Number of Trials to Warm-Up Criteria in the Non-Mnemonic Control condition of the VDT in dogs that preferred the ball. These results suggest that increased IC relates to faster acquisition of a spatial working memory task (which could be due to improved utilization of working memory resources, rule learning or attention). This is the first evidence of a relationship between IC and performance on the controlled version of the VDT which is suggested to measure “purer” spatial working memory processes than the typical version (Krichbaum et al., 2021). This idea is supported by the lack of correlations between SDT and the Regular Study condition of the VDT.

In line with previous studies that found no correlations between tasks to measure IC, there were no relationships between SDT and the Cylinder Task in dogs that preferred the ball or treat (Bray et al., 2014, Brucks et al., 2017; Fagnani et al., 2016; Vernoullit et al., 2018). There are several possible explanations for this finding. First, it was suggested that certain cognitive abilities, in addition to IC, may be important for success on the Cylinder Task (e.g., physical reasoning; Marshall-Picini et al., 2015). For example, dogs require the ability to estimate the distance between themselves and the cylinder, in addition to IC, to be successful on the task. The Cylinder Task is also influenced by other motivational factors (e.g., arousal; Bray et al., 2015) that may not be important in other tests of IC. Second, SDT and the Cylinder Task may be assessing different types of IC (e.g., cognitive and motor, respectively; Riemer, 2014). Additional research is required to determine the validity of the Cylinder Task as a measure of motor IC in dogs however, its usefulness in predicting working dog suitability is evident.

The second aim was to determine the extent to which executive functions relate to detection dog suitability. The relationship between executive functions and detection performance, as assessed by a validated trainer survey (Rooney et al., 2007), revealed a significant negative correlation between Overall Percent Correct in the Cylinder Task and Overall Suitability Scores in dogs that preferred the treat. While this seems to suggest that poorer IC relates to an increase in detection performance, we suggest that this finding can be discussed in terms of arousal. For example, dogs that are more highly aroused perform worse on this task (see Bray et al., 2015 for an example). Given this finding combined with evidence that an increase in work arousal predicts selection as a working dog (Lazarowski et al., 2020b; Lazarowski et al., 2021a), it is likely that these results are merely supporting past conclusions (see Tiiri et al., 2020 for an alternative account). This reasoning can also explain why the relationship was only found in dogs that preferred the treat. Dogs that preferred the ball were so highly aroused that they often did not get a single trial correct (n = 6) and, therefore, there was not enough variance in performance to assess individual differences related to detection dog performance.

We also assessed the relationship between executive functions and another domain of detection dog suitability: environmental soundness (Lazarowski et al., 2021a). As hypothesized, these analyses revealed that an increase in inhibitory control as well as faster acquisition of a working memory task related to better environmental soundness. These findings are the first to suggest that IC and working memory are related to environmental soundness in detection dogs and supports previous work that suggested the relationship between executive functions and emotional reactivity in guide dogs (Bray et al., 2017) as well as the importance of inhibitory control and working memory in the ability to regulate emotions (Foraita et al., 2021).

In contrast to the previous results, we found that better performance in the Cylinder Task was related to greater emotional reactivity in dogs that preferred the treat. This finding supports the idea that the Cylinder Task is assessing motivational rather than IC mechanisms and may be linked to the individual's temperament which is important for selection (Lazarowski et al., 2020a). As discussed earlier, dogs with higher work arousal are more likely to be selected for detection work (Lazarowski et al., 2020b; Lazarowski et al., 2021a) and perform worse on the Cylinder Task (Bray et al., 2015). There is also evidence, based on the Reinforcement Sensitivity Theory of personality, to suggest that higher aroused dogs are bolder allowing them to adapt to novel environments more easily with low levels of inhibition (Piotti et al., 2018b). Additional research should explore the relationship between theories of personality and cognitive performance and their combined effects on detection dog suitability.

Conclusion

We assessed the validity of the SDT to assess IC in dogs and found that while we could rule out the possibility that the task was assessing reward motivation or persistence, SDT did not correlate with another task purported to assess IC: the Cylinder Task. As discussed, there are several explanations for this lack of relationship, however, future research comparing SDT performance to other measures of cognitive IC or validated IC surveys are needed to determine the validity of the SDT. Interestingly, there were relationships between SDT and VDT performance which is the first evidence of a relationship between IC and working memory in dogs. However, additional work is needed to determine the generalizability of these results to other groups of working and companion dogs. In support of past research, we found relationships between executive functions and detection dog suitability. Taken together, these results suggest that detection dogs possess central executive function processes that allow them to perform in difficult situations, navigate high stimulus environments, and engage in goal directed action when approached by fear inducing situations and stimuli. Future work should assess executive functions in early development as this information combined with standard working dog assessments, such as the ERT, could provide a multifaceted approach at predicting detection dog suitability and eventual success.

References

Arden, R., Bensky, M. K., & Adams, M. J. (2016). A Review of Cognitive Abilities in Dogs, 1911 Through 2016: More Individual Differences, Please! *Current Directions in Psychological Science*, *25*(5), 307–312. https://doi.org/10.1177/0963721416667718

Armstrong, R. A. (2014). When to use the Bonferroni correction. *Ophthalmic & Physiological Optics*, 7. https://doi.org/10.1111/opo.12131

Barrera, G., Alterisio, A., Scandurra, A., Bentosela, M., & D'Aniello, B. (2019). Training improves inhibitory control in water rescue dogs. *Animal Cognition*, *22*(1), 127–131. https://doi.org/10.1007/s10071-018-1224-9

Beran, M. J. (2015). The comparative science of "self-control": What are we talking about? *Frontiers in Psychology*, *6*. https://doi.org/10.3389/fpsyg.2015.00051

Brady, K., Cracknell, N., Zulch, H., & Mills, D. S. (2018a). Factors associated with long-term success in working police dogs. *Applied Animal Behaviour Science*, *207*, 67–72. https://doi.org/10.1016/j.applanim.2018.07.003

Brady, K., Hewison, L., Wright, H., Zulch, H., Cracknell, N., & Mills, D. (2018b). A spatial discounting test to assess impulsivity in dogs. *Applied Animal Behaviour Science*, *202*, 77–84. https://doi.org/10.1016/j.applanim.2018.01.003

Bray, E. E., MacLean, E. L., & Hare, B. A. (2014). Context specificity of inhibitory control in dogs. *Animal Cognition*, *17*(1), 15–31. https://doi.org/10.1007/s10071-013-0633-z

Bray, E. E., MacLean, E. L., & Hare, B. A. (2015). Increasing arousal enhances inhibitory control in calm but not excitable dogs. *Animal Cognition*, *18*(6), 1317–1329. https://doi.org/10.1007/s10071-015-0901-1

Brené, S., Bjørnebekk, A., Åberg, E., Mathé, A. A., Olson, L., & Werme, M. (2007). Running is rewarding and antidepressive. *Physiology & Behavior*, *92*(1–2), 136–140. https://doi.org/10.1016/j.physbeh.2007.05.015

Brucks, D., Marshall-Pescini, S., Wallis, L. J., Huber, L., & Range, F. (2017). Measures of Dogs' Inhibitory Control Abilities Do Not Correlate across Tasks. *Frontiers in Psychology*, *8*. https://doi.org/10.3389/fpsyg.2017.00849

Diamond, A. (2013). Executive Functions. *Annual Review of Psychology*, *64*, 135–168. https://doi.org/10.1146/annurev-psych-113011-143750

Erdfelder, E., Faul, F., & Buchner, A. (1996). GPOWER: A general power analysis program. *Behavior Research Methods, Instruments & Computers, 28*(1), 1–11. https://doi.org/10.1146/annurev-psych-113011-143750

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

Foraita, M., Howell, T., & Bennett, P. (2021). Environmental influences on development of executive functions in dogs. *Animal Cognition*, 1-21. https://doi.org/10.1007/s10071-021-01489-1

International Working Dog Registry. Available online: https://www.iwdr.org/bcl/bcl-general-overview/ (accessed on 20 April 2021).

Kelly, D. M., Adolphe, J. L., Vernouillet, A., McCausland, J. A., Rankovic, A., & Verbrugghe, A. (2019). Motoric self-regulation by sled dogs and pet dogs and the acute effect of carbohydrate source in sled dogs. *Animal Cognition*, *22*(6), 931–946. https://doi.org/10.1007/s10071-019-01285-y

Krichbaum, S.**,** Smith G. J., Lazarowski, L., Katz J. S. (2021). Controlling for dogs' (*Canis familiaris*) use of non-mnemonic strategies in a spatial working memory task. *Journal of Experimental Psychology: Animal Learning and Cognition.* https://doi.org/10.1007/s10071-021-01509-0

Lazarowski, L., Haney, P. S., Brock, J., Fischer, T., Rogers, B., Angle, C., Katz, J. S., & Waggoner, L. P. (2018). Investigation of the Behavioral Characteristics of Dogs Purpose-Bred and Prepared to Perform Vapor Wake® Detection of Person-Borne Explosives. *Frontiers in Veterinary Science*, *5*. https://doi.org/10.3389/fvets.2018.00050

Lazarowski, L., Strassberg, L. R., Waggoner, L. P., & Katz, J. S. (2019). Persistence and human-directed behavior in detection dogs: ontogenetic development and relationships to working dog success. *Applied Animal Behaviour Science*, *220*, 104860. https://doi.org/10.1016/j.applanim.2019.104860

Lazarowski, L., Krichbaum, S., Waggoner, L. P., & Katz, J. S. (2020a). The development of problem-solving abilities in a population of candidate detection dogs (Canis familiaris). *Animal Cognition*. https://doi.org/10.1007/s10071-020-01387-y

Lazarowski, L., Waggoner, L. P., Krichbaum, S., Singletary, M., Haney, P., Rogers, B., & Angle, C. (2020b). Selecting Dogs for Explosives Detection: Behavioral Characteristics. *Frontiers in Veterinary Science*, *7*, 597. https://doi.org/10.3389/fvets.2020.00597

Lazarowski, L., Rogers, B., Krichbaum, S., Haney, P., Smith, J. G., & Waggoner, P. (2021a). Validation of a Behavior Test for Predicting Puppies' Suitability as Detection Dogs. *Animals*, *11*(4), 993. https://doi.org/10.3390/ani11040993

Lazarowski, L., Krichbaum, S. (2021b, April 7-10). *Methodological features that influence dogs' detour performance in the cylinder task.* 28th Annual International Comparative Cognition Conference, online conference.

Leighton, E., Hare, L., Thomas, S., Waggoner, L., & Otto, C. (2018). A Solution for the Shortage of Detection Dogs: A Detector Dog Center of Excellence and a Cooperative Breeding Program. *Frontiers in Veterinary Science*, *5*, 284. https://doi.org/10.3389/fvets.2018.00284

MacLean, E. L., & Hare, B. (2018). Enhanced Selection of Assistance and Explosive Detection Dogs Using Cognitive Measures. *Frontiers in Veterinary Science*, *5*. https://doi.org/10.3389/fvets.2018.00236

Marshall-Pescini, S., Virányi, Z., & Range, F. (2015). The Effect of Domestication on Inhibitory Control: Wolves and Dogs Compared. *PLOS ONE*, *10*(2), e0118469. https://doi.org/10.1371/journal.pone.0118469

Mongillo, P., Araujo, J. A., Pitteri, E., Carnier, P., Adamelli, S., Regolin, L., & Marinelli, L. (2013). Spatial reversal learning is impaired by age in pet dogs. *AGE*, *35*(6), 2273–2282. https://doi.org/10.1007/s11357-013-9524-0

Olsen, M. R. (2018). A case for methodological overhaul and increased study of executive function in the domestic dog (*Canis lupus familiaris*). *Animal Cognition*, *21*(2), 175-195. https://doi.org/10.1007/s10071-018-1162-6

Otto, C. M., Cobb, M. L., & Wilsson, E. (2019). Editorial: Working Dogs: Form and Function. *Frontiers in Veterinary Science*, *6*. https://doi.org/10.3389/fvets.2019.00351

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

Perneger, T. V. (1998). What's wrong with Bonferroni adjustments. *BMJ*, *316*(7139), 1236–1238. https://doi.org/10.1136/bmj.316.7139.1236

Piotti, P., Szabó, D., Bognár, Z., Egerer, A., Hulsbosch, P., Carson, R. S., & Kubinyi, E. (2018a). Effect of age on discrimination learning, reversal learning, and cognitive bias in family dogs. *Learning & Behavior*, *46*(4), 537–553. https://doi.org/10.3758/s13420-018-0357-7

Piotti, P., Satchell, L. P., & Lockhart, T. S. (2018b). Impulsivity and behaviour problems in dogs: A Reinforcement Sensitivity Theory perspective. *Behavioural Processes*, *151*, 104–110. https://doi.org/10.1016/j.beproc.2018.03.012

Riemer, S., Mills, D. S., & Wright, H. (2014). Impulsive for life? The nature of long-term impulsivity in domestic dogs. *Animal Cognition*, *17*(3), 815–819. https://doi.org/10.1007/s10071-013-0701-4

Rooney, N. J., Gaines, S. A., Bradshaw, J. W. S., & Penman, S. (2007). Validation of a method for assessing the ability of trainee specialist search dogs. *Applied Animal Behaviour Science*, *103*(1–2), 90–104. https://doi.org/10.1016/j.applanim.2006.03.016

Scott, J. P., & Fuller, J. L. (1965). *Genetics and the Social Behavior of the Dog*. University of Chicago Press.

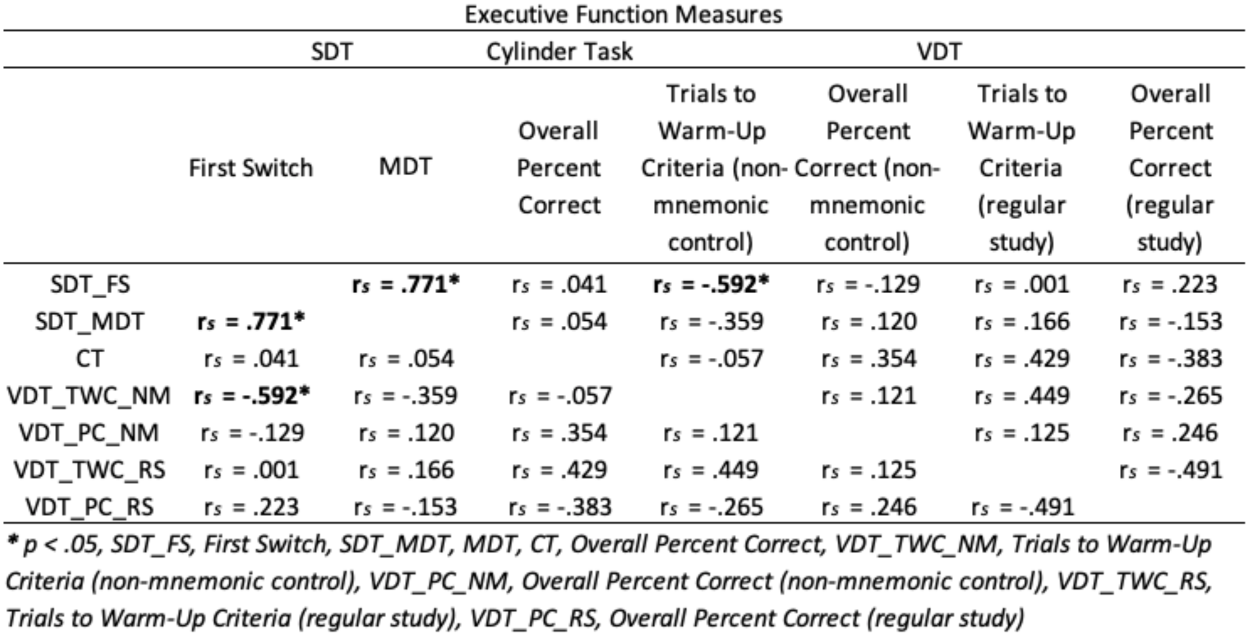
Tapp, P. D., Siwak, C. T., Estrada, J., Head, E., Muggenburg, B. A., Cotman, C. W., & Milgram, N. W. (2003). Size and Reversal Learning in the Beagle Dog as a Measure of Executive Function and Inhibitory Control in Aging. *Learning & Memory*, *10*(1), 64–73. https://doi.org/10.1101/lm.54403

Tiira, K., Tikkanen, A., & Vainio, O. (2020). Inhibitory control – Important trait for explosive detection performance in police dogs? *Applied Animal Behaviour Science*, 104942. https://doi.org/10.1016/j.applanim.2020.104942

Troisi, C. A., Mills, D. S., Wilkinson, A., & Zulch, H. E. (2019). Behavioral and cognitive factors that affect the success of scent detection dogs. *Comparative Cognition & Behavior Review*, *14*, 51–76. https://doi.org/10.3819/CCBR.2019.140007

Vernouillet, A. A. A., Stiles, L. R., Andrew McCausland, J., & Kelly, D. M. (2018). Individual performance across motoric self-regulation tasks are not correlated for pet dogs. *Learning & Behavior*, *46*(4), 522–536. https://doi.org/10.3758/s13420-018-0354-x

Table 1. Spearman correlation matrix between tasks purported to measure executive functions in dogs that preferred the ball.

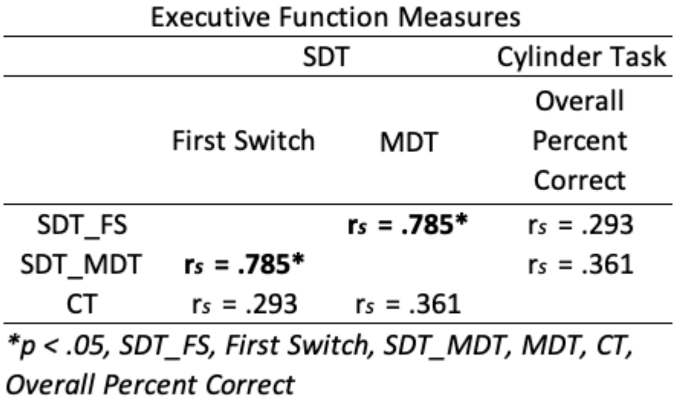


Executive Function Measures

	SDT		Cylinder Task	VDT			
	First Switch	MDT	Overall Percent Correct	Trials to Warm-Up Criteria (non-mnemonic control)	Overall Percent Correct (non-mnemonic control)	Trials to Warm-Up Criteria (regular study)	Overall Percent Correct (regular study)
SDT_FS		**r_s = .771***	r_s = .041	**r_s = -.592***	r_s = -.129	r_s = .001	r_s = .223
SDT_MDT	**r_s = .771***		r_s = .054	r_s = -.359	r_s = .120	r_s = .166	r_s = -.153
CT	r_s = .041	r_s = .054		r_s = -.057	r_s = .354	r_s = .429	r_s = -.383
VDT_TWC_NM	**r_s = -.592***	r_s = -.359	r_s = -.057		r_s = .121	r_s = .449	r_s = -.265
VDT_PC_NM	r_s = -.129	r_s = .120	r_s = .354	r_s = .121		r_s = .125	r_s = .246
VDT_TWC_RS	r_s = .001	r_s = .166	r_s = .429	r_s = .449	r_s = .125		r_s = -.491
VDT_PC_RS	r_s = .223	r_s = -.153	r_s = -.383	r_s = -.265	r_s = .246	r_s = -.491	

***** *$p < .05$, SDT_FS, First Switch, SDT_MDT, MDT, CT, Overall Percent Correct, VDT_TWC_NM, Trials to Warm-Up Criteria (non-mnemonic control), VDT_PC_NM, Overall Percent Correct (non-mnemonic control), VDT_TWC_RS, Trials to Warm-Up Criteria (regular study), VDT_PC_RS, Overall Percent Correct (regular study)*

Table 2. Spearman correlation matrix between tasks purported to measure executive functions in dogs that preferred the treat.



Executive Function Measures

	SDT		Cylinder Task
	First Switch	MDT	Overall Percent Correct
SDT_FS		**r_s = .785***	r_s = .293
SDT_MDT	**r_s = .785***		r_s = .361
CT	r_s = .293	r_s = .361	

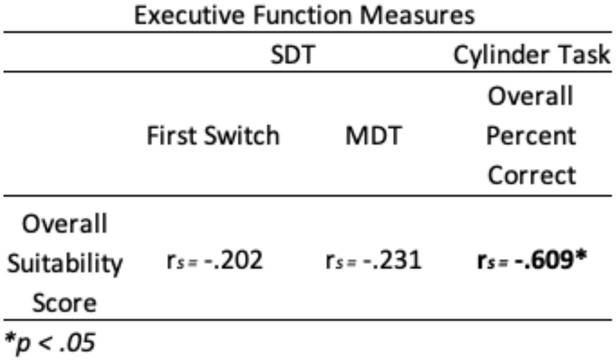
***p < .05, SDT_FS, First Switch, SDT_MDT, MDT, CT, Overall Percent Correct**

Table 3. Spearman correlation matrix between tasks purported to measure executive functions and Overall Suitability Scores in dogs that preferred the ball.

	Executive Function Measures						
	SDT		Cylinder Task	VDT			
	First Switch	MDT	Overall Percent Correct	Trials to Warm-Up Criteria (non-mnemonic control)	Overall Percent Correct (non-mnemonic control)	Trials to Warm-Up Criteria (regular study)	Overall Percent Correct (regular study)
Overall Suitability Score	$r_s = .192$	$r_s = .166$	$r_s = .169$	$r_s = -.082$	$r_s = -.367$	$r_s = -.248$	$r_s = -.052$

*$p < .05$

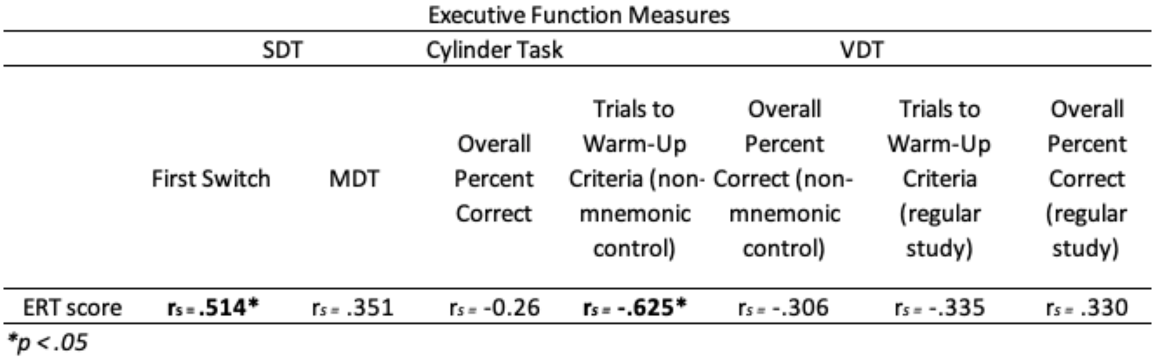
Table 4. Spearman correlation matrix between tasks purported to measure executive functions and Overall Suitability Scores in dogs that preferred the treat.



	Executive Function Measures		
	SDT		Cylinder Task
	First Switch	MDT	Overall Percent Correct
Overall Suitability Score	$r_s = -.202$	$r_s = -.231$	**$r_s = -.609$***

*$p < .05$

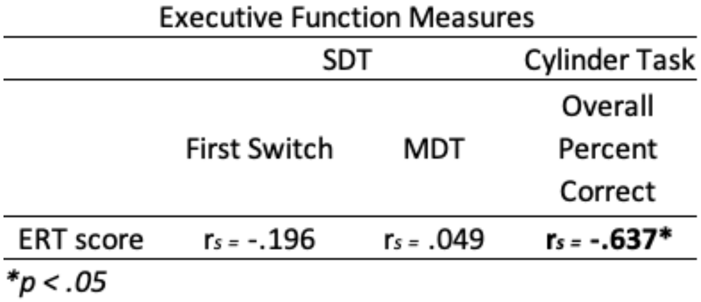
Table 5. Spearman correlation matrix between tasks purported to measure executive functions and ERT Scores in dogs that preferred the ball.



	Executive Function Measures						
	SDT		Cylinder Task	VDT			
	First Switch	MDT	Overall Percent Correct	Trials to Warm-Up Criteria (non-mnemonic control)	Overall Percent Correct (non-mnemonic control)	Trials to Warm-Up Criteria (regular study)	Overall Percent Correct (regular study)
ERT score	**r_s = .514***	r_s = .351	r_s = -0.26	**r_s = -.625***	r_s = -.306	r_s = -.335	r_s = .330

*$p < .05$

Table 6. Spearman correlation matrix between tasks purported to measure executive functions and ERT Scores in dogs that preferred the treat.



Executive Function Measures

	SDT		Cylinder Task
	First Switch	MDT	Overall Percent Correct
ERT score	$r_s =$ -.196	$r_s =$ .049	**$r_s =$ -.637***

******$p < .05$*

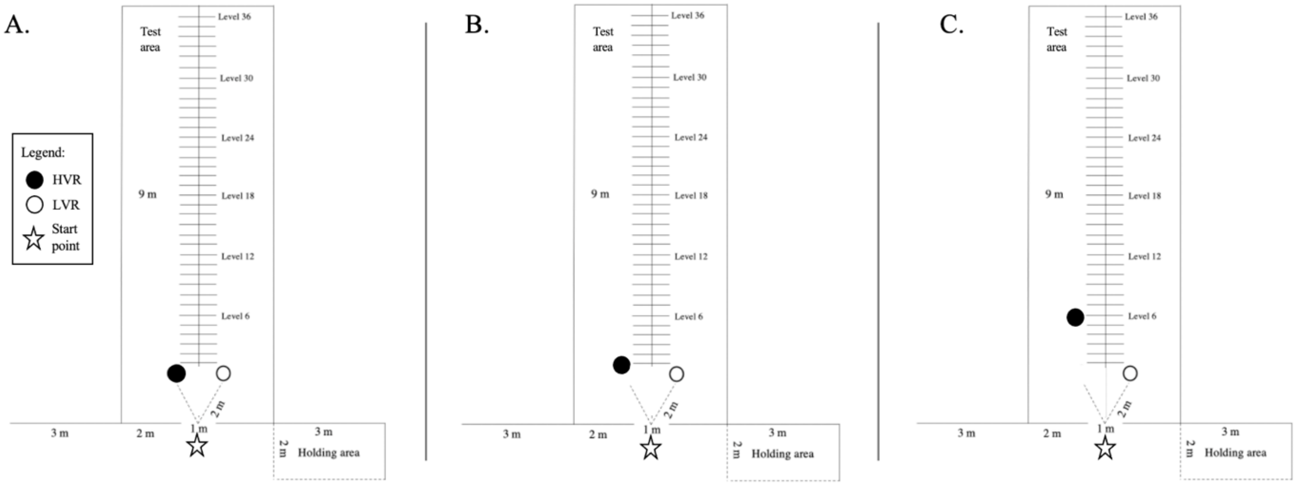


Figure 1. Schematic representation of the SDT apparatus. Panel A represents the experimental set-up for the preference test, Panels B and C represent the hypothetical experimental set-up for trials 1 and 6 of the inhibitory control test, respectively. Tick marks represent ascending levels during the inhibitory control test.

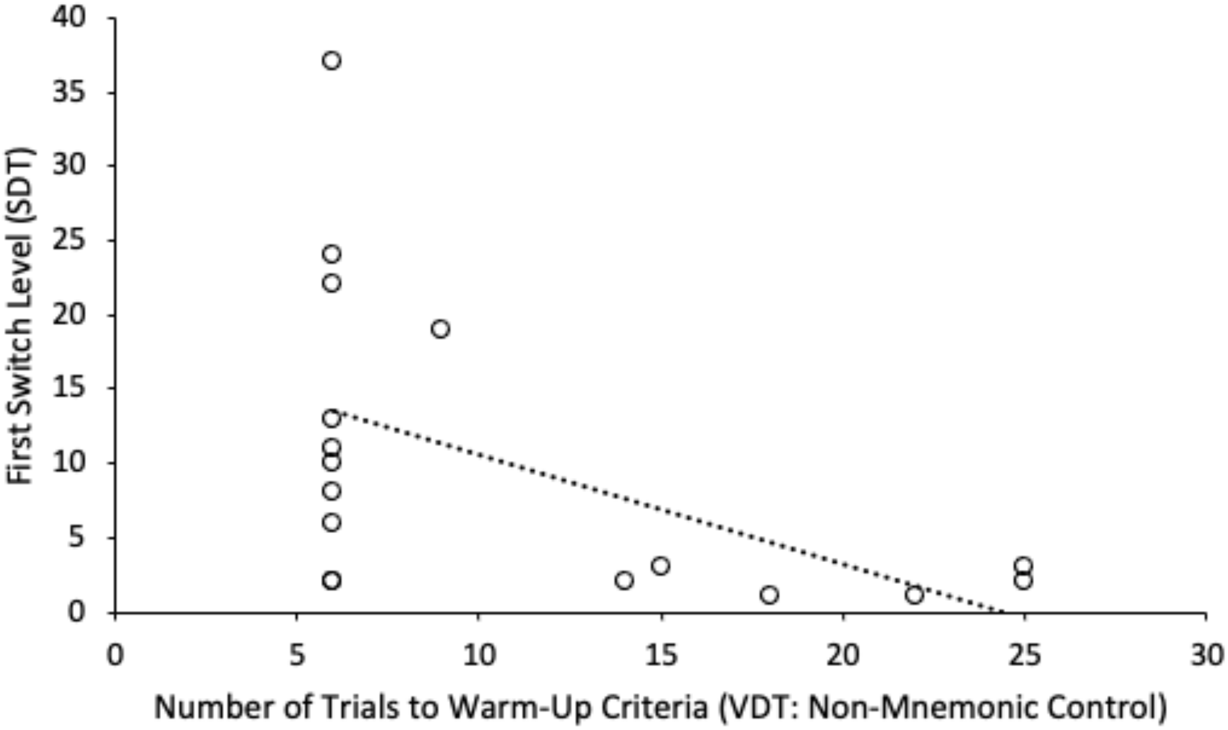


Figure 2. Significant negative correlation between First Switch in the SDT and Number of Trials to Warm-Up Criteria in the Non-Mnemonic Control condition of the VDT in dogs that preferred the ball. Dashed line represents linear trend.

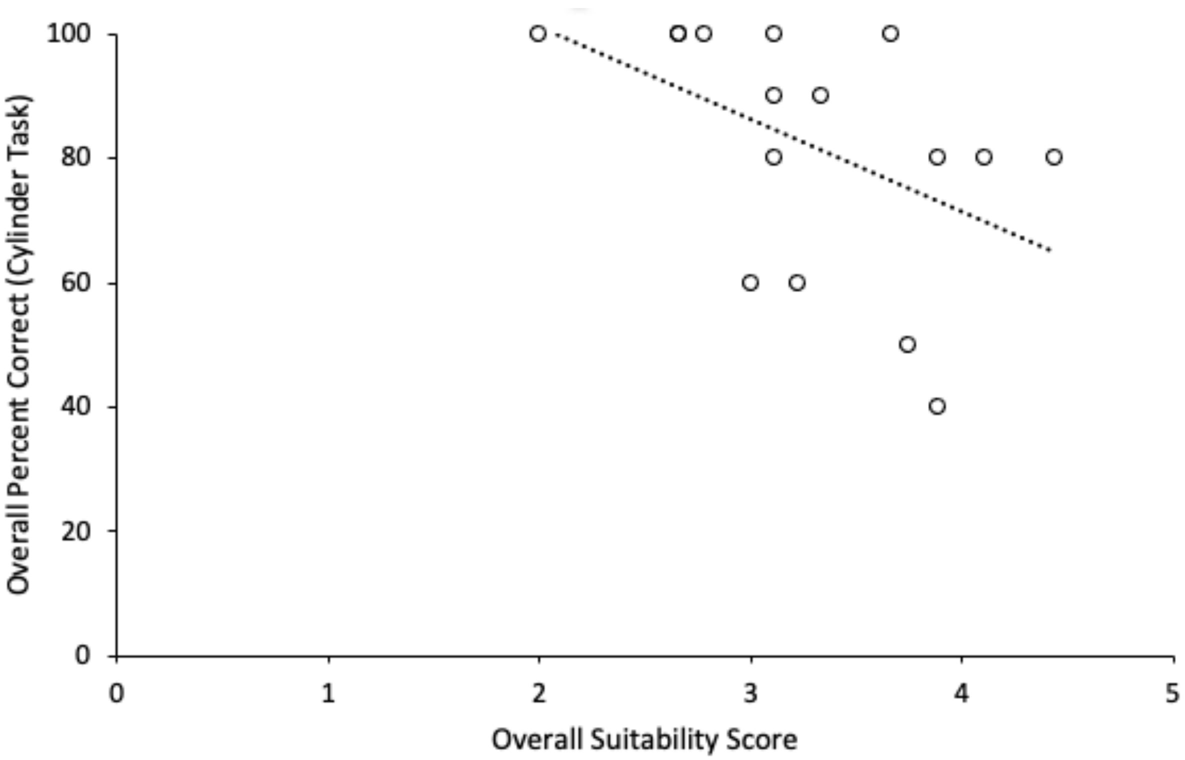


Figure 3. Significant negative correlations between Overall Percent Correct on the Cylinder Task and Overall Suitability Scores in dogs that preferred the treat. Dashed line represents linear trend.

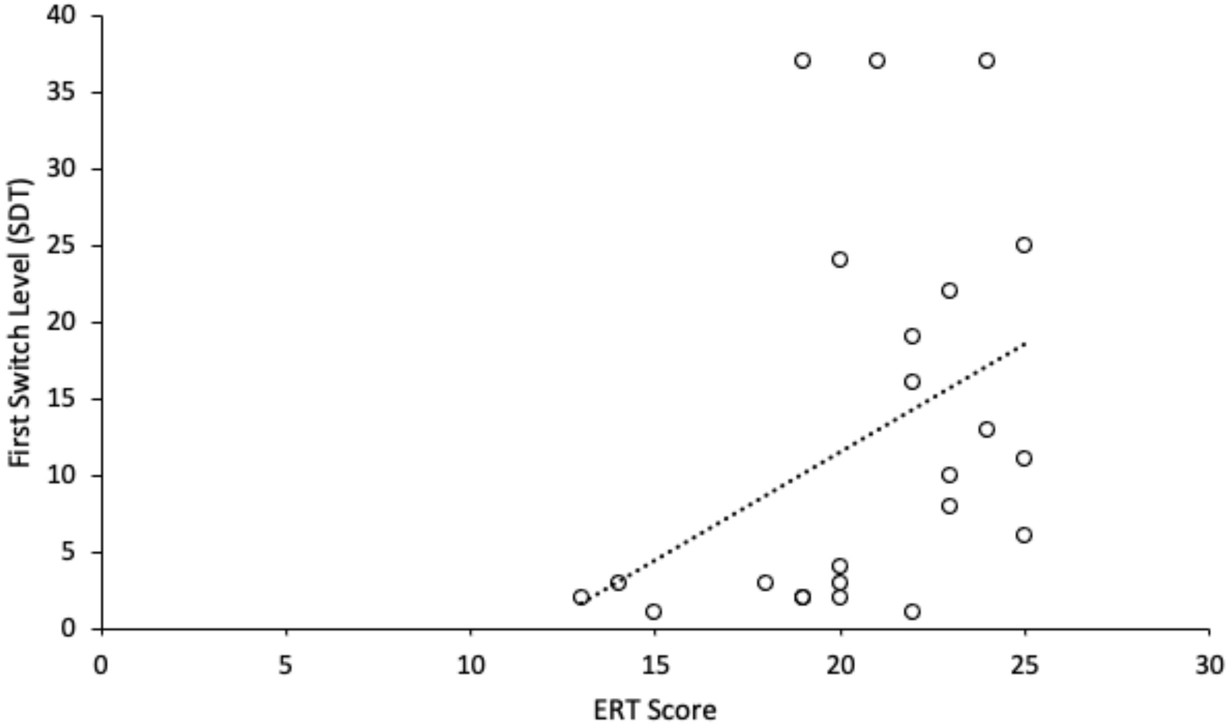


Figure 4. Significant positive correlation between First Switch of the SDT and ERT Scores in dogs that preferred the ball. Dashed line represents linear trend.

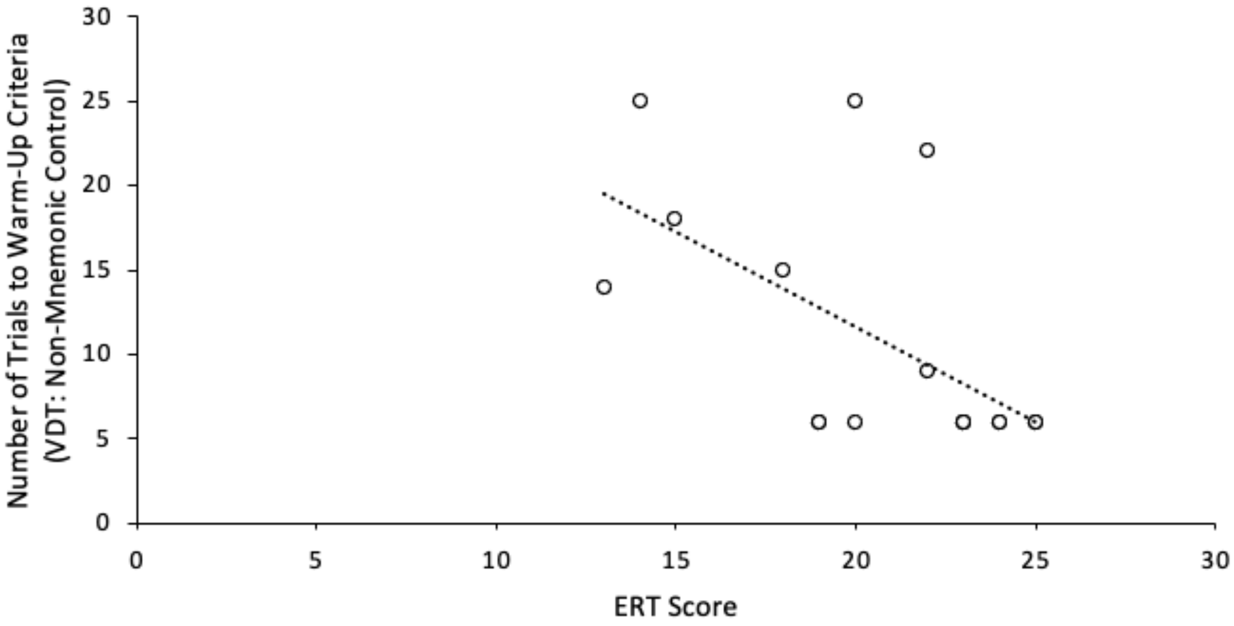


Figure 5. Significant negative correlation between Number of Trials to Criteria in the Non-Mnemonic Control condition of the VDT and ERT Scores in dogs that preferred the ball. Dashed line represents linear trend.

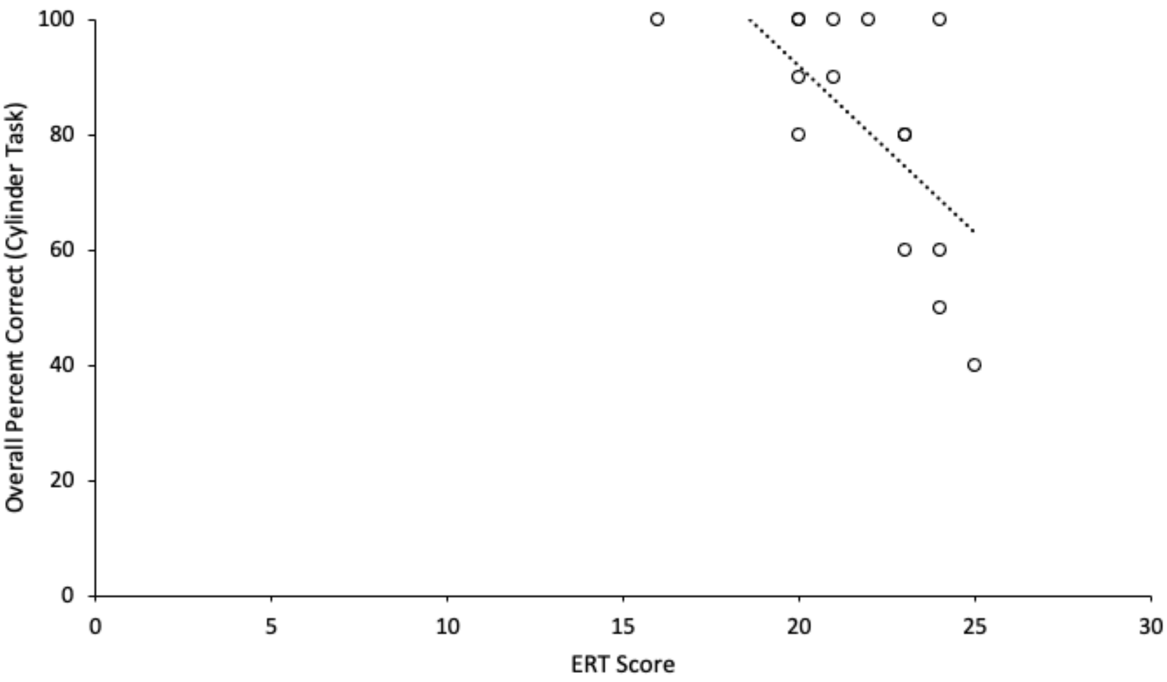


Figure 6. Significant negative correlations between Overall Percent Correct on the Cylinder Task and ERT Scores in dogs that preferred the treat. Dashed line represents linear trend.

Chapter 5: General Conclusions

Canine scientists from around the world have employed single session cognitive tasks (including many used in this dissertation) to answer questions regarding working dog suitability, the translational study of dog and human aging, canine welfare, canine cognition, and comparative cognition. Although these findings are of high importance, their validity as measures of cognitive mechanisms, specifically executive functions, are lacking. The primary aim of this dissertation was to fill gaps in the current literature regarding the validity of tasks used to assess executive functions in dogs and second, to assess their relationship to detection dog suitability. The research within outlines major confounds in the existing literature on canine executive functions, provides ideas for necessary controls in future research, and suggests a strong link between executive functions and detection dog suitability.

Chapter 2 outlines the first study to assess olfactory working memory in dogs using the delayed matching-to-sample-task. I found that dogs performed above chance on delays up to 60 seconds when proactive-interference was essentially non-existent (trial-unique odor set) but that this performance decreased as a function of decreasing set sizes. These results outline the combined effects of delay and proactive interference on dogs working memory for odors and provides a framework for discussing the duration of olfactory working memory compared to working memory of other stimulus modalities in dogs. Implementing this task in groups of detection dogs that specifically rely on scent matching (e.g., tracking dogs) may be useful in determining their working memory limits as well as methods to improve their work.

Chapter 3 takes a direct approach at understanding the confound of non-mnemonic strategies in the visible displacement task (VDT) by assessing dogs' performance in the task on control (non-mnemonic control) and typical (regular study) conditions. I found that performance was lower on the control compared to the typical condition suggesting that the typical VDT, which does not properly control for dogs use of non-mnemonic strategies to solve the task, is not a valid measure of working memory. Therefore, previous research using the VDT should be discussed in terms of dogs' attentional rather than working memory abilities. This assumption was further supported by the positive relationship between the percentage of delay time spent orienting in the direction of the correct stimulus position and overall percent correct on the typical VDT condition.

Lastly, Chapter 4 followed a two-fold focus. First the validity of the Spatial Discounting Test (SDT) as a measure of inhibitory control was assessed by relating dog's performance on the SDT to another measure of inhibitory control (Cylinder Task) and working memory (VDT). In support of previous findings, there were a lack of correlations between tasks purported to measure IC which may be explained by certain motivation factors (e.g., arousal), however, there was a relationship between SDT and VDT performance which is the first evidence to suggest a relationship between inhibitory control and working memory in dogs. Second, the relationship between cognitive tasks to assess executive functions and detection dog suitability was assessed. There was only a relationship between Cylinder Task performance and the performance domain of detection dog suitability, which I believe may be attributable to the importance of arousal on detection dog performance. However, there were relationships between all executive function tasks and the environmental soundness domain suggesting a link between executive functions, emotional regulation, and temperament in dogs. This is the first finding to suggest that tasks to assess working memory and inhibitory control in dogs may be specifically useful for predicting the environmental soundness domain of detection dog work. Future research in this area should combine cognitive tests with behavioral assessments, such as the ERT, to assess this aspect of detection dog suitability.

Future work should consider the above findings when implementing the VDT, SDT, and other tasks purported to assess executive functions in dogs. For example, studies should aim to replicate previous findings on SWM in relation to aging and individual differences using a version of the VDT that controls for non-mnemonic strategies, to determine whether previous results can be attributed to SWM or other processes. There is also a need for continued research to uncover the validity of tasks that measure inhibitory control. These studies should conduct a battery of tasks in a large, controlled (same breed, age, training history, life experiences), population of dogs to determine the mechanisms that these tasks are assessing.

Overall, these results contribute to the current understanding of executive functions in dogs. This dissertation provides insight on dog executive function abilities across stimulus modalities and suggest necessary controls for future work. In addition, it lays a framework for studying the relationship between executive function abilities and detection dog suitability across different domains and suggests specific mechanisms underlying these relationships.