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ARE LARGE DOGS SMARTER THAN SMALL DOGS?

INVESTIGATING WITHIN SPECIES DIFFERENCES

IN LARGE AND SMALL DOGS: SPATIAL MEMORY

by

Megan Samantha Broadway

A Thesis
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ABSTRACT

ARE LARGE DOGS SMARTER THAN SMALL DOGS?

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The study of canine cognition can be useful in understanding the ontology and

selective pressures that affect the development of cognitive abilities. Dogs have

undergone intensive artificial selection yielding distinctive breeds, which differ both

phenotypically and behaviorally. Breed-based cognitive differences have not been found,

but some studies suggest that there may be differences in broader categories such as

working disposition and sex. The influence of size on canine cognition has not been

thoroughly addressed, despite the fact that large dogs are often perceived to be 'smarter'

than small dogs. This preconception has only recently been addressed and supported in

one study comparing large and small dogs in a social cognition task, where large dogs

outperformed small dogs in a pointing choice task. Here, I assessed the cognitive

differences of large and small dogs using a series of spatial cognition tasks. As predicted,

there were no differences between large and small dogs, although small differences were

found between males and females when spay/neuter status was accounted for. Therefore,

it is unlikely that disparities found in social cognition tasks are due to genetic or

physiological differences related to size. Instead, it is probable that differences in

cognitive performance are based on other factors such as prior training experience or past

experience with humans in general.

ACKNOWLEDGMENTS

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CCCAA   Comparative Cognition and Communication Assessment Array

PCTB   Primate Cognitive Test Battery

HSSM   Humane Society of South Mississippi

CHAPTER I

INTRODUCTION

The primary goal of comparative psychology has been to understand how evolution led to advanced cognitive abilities and the role that the social environment played in this process. Our closest living relatives, the great apes, are generally considered to be the most useful species when asking how evolution and ontology resulted in advanced cognition, but other species are proving to be just as important. Species that possess specific abilities of interest, such as an expanded capacity for spatial memory, and also share similar ontological pressures can be valuable in identifying the environmental, behavioral, and ontological factors that fostered that ability. Dogs are one such species.

Dogs are important models for genetic research because of their unparalleled morphometric and behavioral diversity as well as the prevalence of breed-specific diseases (Asher, Diesel, Summers, McGreevy, & Collins, 2009; Galis, Van der Sluijs, Van Dooren, Metz, & Nussbaumer, 2007; Ostrander, 2005; Vaysse et al., 2011). They are also valuable models of behavior and cognition because of their history of domestication and intense enculturation. Based on archeological and genetic evidence, the dog (*Canis familiaris*) originated somewhere between 12,000 and 135,000 years ago (Ovodov et al., 2011; Sablin & Khlopachev, 2002; Savolainen, Zhang, Luo, Lundeberg, & Leitner, 2002; Vilà et al., 1997). It is well accepted that dogs were domesticated from, an ancient form of the grey wolf (*Canis lupis*) (Freedman et al., 2014; Lindblad-Toh et al., 2005; Wayne, 1993), but the location or locations of origin remains a subject of intense debate partly

because of continuous, low levels of cross-breeding throughout history (Vilà et al., 1997; Vilà, Maldonado, & Wayne, 1999; Vilà, Seddon, & Ellegren, 2005).

Dogs have more variation in size, general appearance, and behavior than any other species (Hart, 1995; Wayne, 1986a, 1986b). Physical phenotypic variation includes fur color, texture, and length, body size, leg length, ear type, the amount of curl in the tail, muscularity, and head shape. Dogs also present a wide range of behavioral predispositions including working disposition, energy level, and primary sensory modality. The wide range of physical and behavioral traits present in this species today stems from years of breeding for specific abilities such as hunting, drafting, and companionship, that center around living and working closely with humans (Asher et al., 2009; Roberts, McGreevy, & Valenzuela, 2010).

The behavioral differences between dogs and wolves have long been a subject of interest for researchers but there has been a recent upswing in interest in canine cognition. Much of this interest is likely due to findings that dogs outperform apes on social cognitive tasks (Herrmann, Call, Hernandez-Lloreda, Hare, & Tomasello, 2007) and unlike wolves, dogs look to humans for help when faced with an unsolvable task (Frank & Frank, 1985; Miklósi et al., 2003). These differences have been attributed to dogs' history of domestication (the domestication hypothesis) (Agnetta, Hare, & Tomasello, 2000; Hare, Brown, Williamson, & Tomasello, 2002). The domestication hypothesis suggests that dogs were bred specifically to attend to and cooperate with humans, and this evolutionary history explains their superior performance on social tasks (Agnetta et al., 2000; Hare et al., 2002). More recent evidence suggests that apes can perform at comparable levels on some cognitive tasks when raised in a human

enculturated environment (Lyn, Russell, & Hopkins, 2010; Russell, Lyn, Schaeffer, & Hopkins, 2011), and that dogs may be looking to humans for permission rather than help when they are faced with a seemingly impossible task (Udell, Gibson, & Scavelli, 2013). These findings raise questions regarding the domestication hypothesis; if the performance of apes on social tasks can improve as a result of enculturation and not domestication, enculturation may play a substantial role in canine cognition as well. In addition, recent studies have found that wolves that have undergone intensive enculturation perform as well as dogs on social tasks (Gácsi, Gyoöri, et al., 2009; Miklósi et al., 2003; Udell, Dorey, & Wynne, 2008; Virányi et al., 2008) and that dogs raised with restricted human contact do not perform above chance on social tasks (Lazarowski & Dorman, 2015; Udell, Dorey, & Wynne, 2010). If dogs and wolves are not as different as originally thought, then enculturation, not domestication, may be the primary factor involved in advanced social cognitive abilities.

Researchers often study breed comparisons in order to assess cognitive differences that may have developed due to selection for specific behavioral traits. A few of these studies have focused on breed differences using social tasks involving the comprehension of communicative gestures (e.g. Gácsi, McGreevy, Kara, & Miklósi, 2009; Helton & Helton, 2010; Wobber, Hare, Koler-Matznick, Wrangham, & Tomasello, 2009). Other cognitive abilities, such as spatial memory and object permanence, have received much less attention as these abilities seem to be relatively consistent in dogs and wolves (Fiset & Plourde, 2013). However, it is important to assess basic cognitive abilities, such as spatial memory along with social cognition, when comparing breeds or any other within species comparison.

Some breeds, or breed categories, are perceived to be more cognitively capable than others; therefore, breed comparisons are often examined before considering more obvious differences such as size. Although there are perceived differences in intelligence among breeds, testing has revealed little difference in physical or social cognition, possibly do to low sample sizes (e.g. Gagnon & Doré, 1992; Jakovcevic, Elgier, Mustaca, & Bentosela, 2010; Wobber et al., 2009). Where studies comparing breeds have failed, comparisons between broader categories have revealed some potential cognitive differences. For example, initial studies utilizing the pointing choice task have found that: cooperative working breeds outperform independent workers (Jakovcevic et al., 2010), dogs with a wider skulls perform better than those with an elongated skull (Gácsi, McGreevy, et al., 2009), and large dogs outperform small dogs (Helton & Helton, 2010). Comparisons of males and females have shown mixed results (Duranton, Rödel, Bedossa, & Belkhir, 2015; Müller, Mayer, Dörrenberg, Huber, & Range, 2011; Müller, Riemer, Range, & Huber, 2014).

Judgments regarding intelligence are generally based on how well members of that breed respond to training (Helton, 2009; Turcsán, Kubinyi, & Miklósi, 2011). Dogs that can learn new and complicated behaviors quickly are perceived to be clever whereas, independent or stubborn dogs that are not easily trained are perceived to be unintelligent (Bailey, 1986). Herding breeds like the Australian Shepard and Border collie rank high in perceived trainability (Coren, 1994) whereas most companion breeds, which tend to be small dogs, do not (Draper, 1995; Ley, Bennett, & Coleman, 2009; Turcsán et al., 2011). Smaller dogs are also more likely to be perceived as neurotic, intolerant of others, and introverted - traits which are negatively correlated with motivation and trainability (Ley

et al., 2009). As a result, small dogs are perceived to be less trainable and, therefore, less intelligent while large dogs are perceived to be cognitively superior to small dogs even though there is no evidence to support this claim (Helton, 2010).

Size in dogs is regulated by a small set of genes (Boyko et al., 2010; Hoopes, Rimbault, Liebers, Ostrander, & Sutter, 2012; Jones et al., 2008; Rimbault et al., 2013; Sutter et al., 2007), particularly the IGF1 allele (Hoopes et al., 2012; Sutter et al., 2007). This haplotype is present only in small dog breeds with the exception of a few large breeds, namely the Rottweiler (Sutter et al., 2007). Oddly, it is not present in the nearest evolutionary relative, the Grey wolf, or any other candid species meaning that this form of the gene that was present in the common ancestor (Freedman et al., 2014) or is the result of a mutation that occurred after the domestication process began (Gray, Sutter, Ostrander, & Wayne, 2010).

The classification of 'small' is somewhat objective as size categories are not specified by the various breeding authorities such as the American Kennel Club. In many studies that have compared small and large dogs, dogs were classified according to weight, with small dogs typically listed as being less than 9.9 or 10 kg (22 lbs) by actual or breed standard weight and large dogs ranging from >10 kg to >90 kg (Gray et al., 2010; Helton & Helton, 2010; Jakovcevic et al., 2010; Sutter et al., 2007; Taylor, Reby, & McComb, 2010). Several studies also classified size according to shoulder height, with the small dog group having a shoulder height of < 43cm and the large dog category ranging from >43 cm to >69 cm (Gagnon & Doré, 1992; Li, Deeb, Pendergrass, & Wolf, 1996).

Intense selective breeding for size led to unintended consequences, particularly for very large and very small dogs, such as increased risk for degenerative diseases and developmental disorders (Asher et al., 2009). Many of the health issues for these animals stem from problems relating to development and growth (see Galis, Van der Sluijs, Van Dooren, Metz, & Nussbaumer, 2007). For example, very large dogs tend to have a shortened lifespan with some of the largest breeds living an average of only six years, most likely due to the high rate of growth early in life (see Galis, Van der Sluijs, Van Dooren, Metz, & Nussbaumer, 2007). There are other differences caused by size as well. Small dogs have a larger tooth to body size ratio than large dogs (Wayne, 1986a), they have comparatively larger organs, and have larger pups relative to adult size (Kirkwood, 1985).

Changes in skull morphology are responsible for a range of sensory and possibly cognitive differences and are also correlated with size differences in dogs (Gácsi, McGreevy, et al., 2009; Gittleman, 1991; McGreevy, Grassi, & Harman, 2004; Roberts et al., 2010). Wolves are considered to be dolichocephalic, meaning they have an elongated skull, but selective breeding has pushed this to the extreme. Dogs such as greyhounds, which were bred for speed, developed a more aerodynamic form including long, lean legs and an elongated head resulting in extreme dolichocephaly. Selective breeding has also worked in the opposite direction creating dogs like the pug and Pekinese with a shortened skull and almost no snout at all, a condition known as brachycephaly. Selection for a particular feature or ability often led to deficits in other abilities due to co-occurring structural changes. For example, breeds like bulldogs and pugs, which were bred to have

a shortened muzzle, also have a restricted airway and as a result have a decreased sense of smell (Koch, Arnold, Hubler, & Montavon, 2003; Roberts et al., 2010).

Differences in dolichocephalic and brachycephalic skulls have been documented (Evans & Christensen, 1979) but the brain itself has received little attention despite obvious differences (Roberts et al., 2010). In terms of structural changes, the most prominent difference is the positioning of the olfactory bulb which is located in the orbital frontal cortex in brachycephalic dogs and near the frontal lobe in dolichocephalic dogs (Roberts et al., 2010). This repositioning is assumed to be a space-saving mechanism to preserve the size of frontal cortex (Roberts et al., 2010); although direct comparisons of dolichocephalic and brachycephalic brain regions have yet to be performed.

A less obvious difference between skull types involves differences resulting from the positioning of the eyes. The heads of brachycephalic dogs are broader which causes the eyes to face forward and contributes to a more juvenile appearance (Wayne, 1986a, 2001). Alternately, the heads of dolichocephalic dogs are more narrow which causes the eyes to be located slightly laterally, on either side of the head. As a result, the distribution of ganglion cells in the retina is correlated with skull morphology with brachycephalic dogs having a centrally located, circular cell distribution similar to humans, and dolichocephalic dogs having a horizontal strip of cells (McGreevy et al., 2004), a trait they share with the grey wolf (Miller & Murphy, 1995; Peichl, 1992a, 1992b). Because brachycephaly is more common in small dogs (Evans & Christensen, 1979; Roberts et al., 2010; Wayne, 2001), they are more likely to have a circular ganglion cell distribution whereas larger dogs would be more likely to have a horizontal ganglion cell distribution.

The effect this has on vision has not been tested, but because the eyes face forward in animals with a brachycephalic head shape, animals with broader skulls are likely to have better binocular vision as well; although there is some disagreement as to whether this is true for both large and small dogs (Helton & Helton, 2010). This indicates that brachycephalic dogs may have increased central visual resolution and decreased peripheral vision compared to dolichocephalic dogs (Helton & Helton, 2010). More centrally focused vision would allow the animal to focus on what is directly in front of them at near or far distances with better depth perception (Allison, Gillam, & Vecellio, 2009), and restricted peripheral vision would help to lessen visual distractions. In combination, these characteristics would presumably aid in the ability to focus attention on human communicative gestures (McGreevy et al., 2004). Gácsi et al., (2009) tested this hypothesis behaviorally and found that brachycephalic dogs performed significantly better (~80% correct) on a pointing choice task than dolichocephalic dogs (~60% correct). As others have suggested (McGreevy et al., 2004), Gácsi et al., (2009) attributed the differences in performance to the superior ability of brachycephalic dogs to attend and focus on the communicative signals of humans.

Because brachycephaly is more common in smaller dogs, it stands to reason that as a group, small dogs would have better central vision and possibly better attentive abilities than large dogs. However, Helton and Helton (2010) compared the performance of small (<22.7 kg) and large (>22.7 kg) dog breeds on a pointing choice task and found that the opposite was true. In this study, data were taken from a larger study by Gácsi et al. (2009), comparing different breeds of dog on the pointing choice task. Helton and Helton (2010) analyzed data from 104 dogs and found that large dogs performed

significantly better than small dogs on the task. The researchers also broke this down further to compare small (<27 lbs), medium (27 - 67.5 lbs) and very large (>67.5 lbs) dogs with brachycephalic dogs removed and found that medium and large dogs performed significantly better than small dogs (Helton & Helton, 2010). Large dogs may have performed better due to several factors that could overcome the dolichocephalic disadvantage (Helton & Helton, 2010).

For example, the superior performance of large dogs could have been due to differences in inter-ocular spacing because as inter-ocular distances shrink, as is the case with smaller dogs, stereopsis and depth perception suffer (Allison et al., 2009; Changizi & Shimojo, 2008; Helton & Helton, 2010) leaving small brachycephalic dogs at a disadvantage. Large brachycephalic dogs would not be affected by this phenomenon because the inter-ocular spacing of large dogs is adequate (Helton & Helton, 2010). Even though small dogs are more likely to have the benefit of forward facing eyes and better binocular vision, their small size also causes them to have reduced inter-ocular spacing (Helton & Helton, 2010). Therefore, theoretically, the vision of small dogs may be more monocular than binocular which would cause them to have even poorer visual acuity than dolichocephalic large dogs

Previous experience is also a factor that could have affected performance (Helton & Helton, 2010; Wynne, Udell, & Lord, 2008). The effect of previous experience is a legitimate confound in comparative research that is often erroneously applied in a very narrow sense (see Lyn, Russell, & Hopkins, 2010; Russell, Lyn, Schaeffer, & Hopkins, 2011), such as the animal's previous experience with a particular task. The animal's previous living experience with humans is often ignored. Small and large dogs are often

treated differently and receive different levels of training, with larger dogs receiving more training and attention with regard to communicating effectively with humans (Kobelt, Hemsworth, Barnett, & Coleman, 2003). Disobedience in small dogs is often perceived to be harmless and is tolerated without consequence, whereas large dogs that perform those same behaviors are considered intolerable or even dangerous (Bennett & Rohlf, 2007; Helton & Helton, 2010). Therefore, more effort is typically devoted to training large dogs. Thus, the previous experience that large dogs have with humans may give them an advantage in solving cognitive tasks in that they are more likely to be accustomed to understanding the intentional cues of humans. If these attempts fail the consequences can be less than ideal for the dog which may be rehomed, abandoned, or even destroyed.

Dogs that work cooperatively with humans have been shown to outperform other types of dogs on some cognitive tasks (Gácsi, McGreevy et al., 2009), so one final explanation is that small dogs performed poorly because they were not bred to work closely with humans (Helton & Helton, 2010; Wobber et al., 2009). Instead, small dogs were bred to be either companion animals, such as the Papillion and Havanese, or to work independently from humans - the dachshund for example, which was bred to hunt small burrowing animals without human cueing. Dogs that were bred to work cooperatively with humans, such as gundogs and herding dogs, tended to be larger breeds. This unequal distribution of cooperative and non-cooperative working dogs can make comparisons between working disposition and size difficult when trying to achieve a balanced group design. For example, in the Gácsi et al., (2009) study, cooperative workers significantly outperformed both independent workers, and mixed breed

"mongrels" on a pointing choice task. Descriptions of the mongrels were not listed; therefore, size estimates for the mongrel group could not be determined. However, there were more small dogs in the independent group than the cooperative worker group. Because Helton and Helton's (2010) study was based on a previous set of data comparing the effects of working disposition as well as skull morphology in a pointing task (Gácsi et al.'s, 2009), it is highly likely that Helton and Helton's (2010) small dog group had more independent workers and the large dog group had more cooperative workers. This confounding factor could have influenced Helton and Helton's (2010) results.

Similarly, Wobber et al. (2009) compared working dogs to non-working dogs and found that working dogs performed significantly better than non-working dogs on various communicative and cued tasks, including a pointing choice task. In this case, the working breeds tested consisted of shepherds (German and Belgian) and Siberian huskies while the non-working breeds were toy poodles and basenjis. The working breeds range from 16 to 43 kg while the non-working breeds that were used ranged from 6 to 11 kg (Fogle, 1995). Therefore, like Gácsi et al. (2009) and Helton and Helton (2010), Wobber et al. (2009) inadvertently compared not only working and non-working dogs, but also small and large dogs, possibly confounding the results. With all three of these studies comparing either size or working disposition (Gácsi, McGreevy et al., 2009; Helton & Helton, 2010; Wobber et al., 2009), the results were consistent with large dogs outperforming small dogs on the pointing choice task and working dogs outperforming non-working dogs. However, due to the confounding factors of size and working status, the determination of each variable's influence on cognitive performance is unclear. As suggested by Helton and Helton (2010), the physical characteristics of the dogs, as well

breed differences, should be controlled for in testing. If size does influence canine cognition, group designs balanced for size should be employed for cognitive studies with dogs.

<div align="center">Spatial Memory in Dogs</div>

Spatial memory and object permanence abilities are thought to be the basis for many higher level cognitive functions (Jaakkola, Guarino, Rodriguez, Erb, & Trone, 2009; Pollok, Prior, & Güntürkün, 2000)**.** The ability to recognize that an object still exists even though it has moved out of sight is a basic cognitive skill that is necessary for the formation of mental representations. But not all species possess these abilities to the same degree. Jean Piaget (1937/1954) was the first to delve into the complexity of these abilities and dissect them into a progression of stages, each building on the last. Piaget (1937/1954) identified six different stages of competence and created a series of tasks to test the development of each stage in children.

These tasks were later used to test object permanence abilities in animals (see Jaakkola et al., 2009). Many of the species investigated have demonstrated the ability the solve visible displacement tasks where the subject watches as an object is hidden in, behind, or under an occluder and is then allowed to retrieve the object. Various species of ape (Call, 2001; de Blois, Novak, & Bond, 1998, 1999; Mathieu, Bouchard, Granger, & Herscovitch, 1976; Minahan, Beran, & Savage-Rumbaugh, 2000; Natale, Antinucci, Spinozzi, & Potí, 1986; Russell et al., 2011; Spinozzi & Potí, 1993), monkey (de Blois et al., 1999; de Blois & Novak, 1994; Deppe, Wright, & Szelistowski, 2009; Hauser, Williams, Kralik, & Moskovitz, 2001; Hauser, 2001; Mathieu et al., 1976; Mendes & Huber, 2004; Neiworth et al., 2003), canid (Gagnon & Doré, 1992, 1993, 1994; Triana &

Pasnak, 1981), cat (Doré, 1986; Dumas & Doré, 1989, 1991; Goulet, Doré, & Rousseau, 1994; Thinus-Blanc, Poucet, & Chapuis, 1982; Triana & Pasnak, 1981), bird (Bugnyar, Stöwe, & Heinrich, 2007; Funk, 1996; Hoffmann, Rüttler, & Nieder, 2011; Pepperberg, Willner, & Gravitz, 1997; Pepperberg & Funk, 1990; Pepperberg & Kozak, 1986; Pollok et al., 2000; Zucca, Milos, & Vallortigara, 2007), hamster (Thinus-Blanc & Scardigli, 1981), and bottlenose dolphin (Jaakkola et al., 2009; Johnson, Sullivan, Buck, Trexel, & Scarpuzzi, 2014) have been successful in visible displacement tasks.

However, the sixth stage of Piagetian object permanence involves understanding of invisible displacement - the ability to infer the final position of a hidden object that has been invisibly relocated based on visual contextual clues (Piaget, 1937/1954). Very few species have demonstrated the ability to solve invisible displacement problems of any kind. Great apes are the only group found to be capable of consistently solving these tasks (Barth & Call, 2006; Call, 2001; Collier-Baker & Suddendorf, 2006; de Blois et al., 1998, 1999; Mathieu & Bergeron, 1981; Mathieu et al., 1976; Minahan et al., 2000; Natale et al., 1986; Natale, 1989; Redshaw, 1978; Russell et al., 2011). Other species that have shown some ability to solve invisible displacement tasks include psittacine birds (Funk, 1996; Pepperberg & Funk, 1990; Pepperberg & Kozak, 1986; Pepperberg et al., 1997) and corvids (Bugnyar et al., 2007; Hoffmann et al., 2011; Pollok et al., 2000; Zucca et al., 2007), but it has been questioned as to whether these species used mental representational or some other strategy to solve these tasks (Jaakkola et al., 2009; Mallavarapu, Perdue, Stoinski, & Maple, 2013; Pollok et al., 2000).

Cognitive ability can be investigated using a variety of methodologies and the Piagetian tasks are not the only tasks used to assess object permanence in animals.

Visible displacement in dogs has been investigated using a maze (Frank & Frank, 1987; Macpherson & Roberts, 2010), barriers (Frank & Frank, 1987), locomotion tasks (Cattet & Etienne, 2004), and variations of Piagetian tasks (Fiset & Plourde, 2013; Gagnon & Doré, 1992, 1993, 1994; Triana & Pasnak, 1981). Tests can vary not only by task but by the innumerable variations that can intentionally or unintentionally be incorporated into the methodological procedures for each task (Barth, Reaux, & Povinelli, 2005; Boesch, 2007). Seemingly small procedural variations can have drastic effects on a subject's ability to successfully complete a task (e.g. Deák, Flom, & Pick, 2000; Hattori, Kuroshima, & Fujita, 2010; Lyn et al., 2014; Moore & D'Entremont, 2001). This problem has proven to be particularly cumbersome in studies of spatial memory and object permanence in dogs. For example, dogs do not perform above chance on radial maze or barrier tasks, but they were capable of solving visible displacement tasks when tested using Piagetian style tasks (Cattet & Etienne, 2004; Fiset & Plourde, 2013; Gagnon & Doré, 1992, 1993, 1994; Macpherson & Roberts, 2010; Triana & Pasnak, 1981). In addition, studies of invisible displacement in dogs have shown mixed results even when similar Piagetian style tasks were used (Collier-Baker, Davis, & Suddendorf, 2004; Fiset & Leblanc, 2007; Fiset & Plourde, 2013; Gagnon & Doré, 1992, 1993, 1994; Rooijakkers, Kaminski, & Call, 2009; Triana & Pasnak, 1981; Watson et al., 2001).

When first tested, dogs were able to solve Piagetian style invisible displacement problems (Gagnon & Doré, 1992, 1993, 1994; Triana & Pasnak, 1981). Although questioned (Doré & Dumas, 1987; Doré, Fiset, Goulet, Dumas, & Gagnon, 1996; Doré & Goulet, 1998), this finding was upheld until it was reassessed by Collier-Baker et al., (2004) who found that the dogs were using simple associative rules based on the final

location of the displacement device. Dogs were only successful in locating the hidden

reward if the initial container's final location was placed adjacent to the correct occluder

(Collier-Baker et al., 2004). Instead of using mental representation to solve the task, the

dogs appeared to be using the initial container as an external cue (Collier-Baker et al.,

2004). Others have replicated these findings demonstrating that dogs do not perform

above chance on Piagetian style invisible displacement tasks (Fiset & Leblanc, 2007).

Dogs have also been unsuccessful in other invisible displacement tests. The

rotation task involves hiding an object in one of a series of two to three occluders and

then rotating the entire arrangement up to 360 degrees. Only a few studies have utilized

this task with dogs. Dogs failed a 180° rotation task utilizing a platform with three

containers, one on each end and one in the middle (Fiset & Plourde, 2013). In a less

complicated experiment, Miller, Gipson, Vaughan, Rayburn-Reeves, & Zentall (2009)

placed an object in one of two containers on a platform then rotated the arrangement

either 180 or 90 degrees. Dogs failed the 180° rotation but correctly located the object on

90° rotation trials. Miller et al. (2009), also altered this task so that the object was hidden

in one of the two containers; however, instead of rotating the platform, the dog was led

around the arrangement so that the location of the containers was rotated according to the

dog's perspective. Dogs were successful on these trials leading the authors to believe that

the lack of change in contextual clues may have influenced the dogs' poor performance

on the initial 180° rotation task (Miller et al., 2009).

Transposition is an invisible displacement task which can be considered more

straight forward than the Piagetian task because the displaced object remains hidden by

the same occluder the entire time (Doré et al., 1996). Children find this task to be more

difficult to solve than the Piagetian invisible displacement tasks, but surprisingly, apes do not (Barth & Call, 2006). Several studies have used transposition tasks to provide clear evidence that dogs are strongly influenced by the initial position in which the object is hidden (Doré et al., 1996; Fiset, Gagnon, & Beaulieu, 2000; Fiset & Plourde, 2013; Rooijakkers et al., 2009), a hypothesis that has also been suggested from work with Piagetian style tasks (Fiset & Leblanc, 2007). In these studies, an object is hidden in or behind an occluder and then the occluder is moved to another possible location. In substitution transposition tasks there is one more location than the number of occluders so that one location remains unoccupied at all times. In these tasks dogs perform better when the location in which the object was first hidden is unoccupied after transposition which suggests that dogs show a strong bias toward the object's initial location (Doré et al., 1996; Fiset & Plourde, 2013; Rooijakkers et al., 2009). Another form of transposition task involves hiding a reward and then switching the order of the occluders, as is done in the "shell game." Rooijakkers et al. (2009) postulated that dogs were affected by the crossing of containers during these tasks. It has been suggested that dogs use the location of the experimenter as a landmark in situations where the target location is adjacent to the experimenter; however this situation occurs in only a portion of test trials and not all dogs make this association during testing (Fiset & Leblanc, 2007).

<div align="center">Cognitive Comparisons in Large and Small Dogs</div>

There have been no comparisons between the performance of small and large dogs on spatial memory and object permanence tasks, but such comparisons have been conducted for one social cognition task. Large dogs performed better than small dogs on a pointing choice task (Helton & Helton, 2010). In addition to the confounding factor of

working and non-working breeds already described, the better performance of large dogs may have been due to one other factor that was not addressed. Müller, Mayer, Dörrenberg, Huber, and Range, (2011) found that female dogs performed significantly better than males on an object permanence size consistency violation task. The proportion of male and female dogs used for each group in the Helton and Helton (2010) study was not provided. If groups were not balanced in the number of male and female dogs, this could have affected the results.

The influence of size on canine cognition has not been thoroughly addressed despite the fact that large dogs are perceived to be 'smarter' than small dogs. With this study we hope to determine if large dogs outperform small dogs on visible and invisible displacement tasks. Dogs and wolves have been found to perform equally on spatial cognitive tasks (Fiset & Plourde, 2013) meaning that it is unlikely that selection pressures during domestication influenced spatial cognition in dogs. Therefore, I hypothesize that large and small dogs will perform equally on a variety of visible and invisible displacement tasks. If large dogs outperform small dogs, this could confirm the perception that large dogs are smarter than small dogs and would lend some support to the finding that large dogs are superior in solving social tasks (Helton & Helton, 2010). Alternately, negative findings could be a result of physical limitations such as differences in inter-ocular distance, ontological differences and previous experiences with humans, or actual cognitive differences. If negative results are due to cognitive differences, this could be an example of the early evolution of spatial cognition within the species *Canis familiaris*.

CHAPTER II

METHODS

A sub-section of the Comparative Cognition and Communication Assessment Array (CCCAA) was used to test spatial memory, object permanence, and transposition abilities in small and large dogs. The CCCAA is based on the Primate Cognitive Test Battery (PCTB) that was originally developed by (Herrmann et al., 2007). The PCTB included tasks to test complex cognitive abilities that were broken into two types: physical and socio-cultural cognition. Physical cognition skills included spatial cognition, numerosity, tool use, and causality, while socio-cultural cognition included skills like social learning, communication, and theory of mind. The categories of physical and social cognition were highlighted in the original PCTB in order to compare the abilities of pre-school aged children and apes. It was hypothesized that children would perform better on social tasks due to an innate ability. The conclusions of the authors were criticized on several levels, including methodology and interpretations (De Waal, Boesch, Horner, & Whiten, 2008); however, the premise of assessing cognitive skills systematically and with truly comparative methods remains valid. Additionally, using multiple testing methods to assess a particular ability can guard against false positive or false negative conclusions that are formed based on the results of one particular task.

The CCCAA was created to test cognitive abilities and to adapt tasks for use with animals that have different primary sensory modalities and to be adaptable for animals that use body parts other than forelimbs to maneuver objects. Like the PCTB, the full CCCAA has two main sections, physical cognition and socio-cultural cognition. Many of these tasks proceed in increasing levels of difficulty and can be assessed by the

developmental age at which humans master the task. For example, spatial tasks begin with simply locating an object (by watching the item being hidden and choosing the correct container), and increase in difficultly to end with invisible displacement where the participant must consciously attend to a hidden object as it is moved from one hidden location to another.

<div align="center">Subjects</div>

Testing of shelter dogs was conducted at the Humane Society of South Mississippi (HSSM) located in Gulfport, Mississippi. This shelter houses over 2,000 dogs annually, each with an average stay of approximately one week for small dogs and four months for large dogs. A total of 84 dogs began testing, but only 33 completed all 13 tasks. Another three data points were created by combining partial data from a total of six dogs that completed a portion of the tasks by matching dogs that had similar characteristics which included size, sex, alteration status and breed type. This resulted in complete data sets for a total of 36 subjects (including matches), 17 large ($\geq$ 18 kg, 8 male, 9 female) and 19 small ($\leq$ 9 kg, 9 male, 10 female). All dogs were one year of age or older (see Gagnon & Doré, 1994).

Unlike most other studies, weight was not determined by breed standard weight because the animals that are housed at the HSSM are rarely pure breed dogs. Instead, the weight of each individual subject was used to determine size classification. To control for breed types, each size and sex grouping consisted of mixed working and non-working, breed dogs. The categorization of working or non-working breed was determined by a combination of the HSSM intake assessment and the discretion of the researchers.

Table 1

Description of Subjects

Name	Size	Sex	Altered	Weight (kg)	Weight (lbs)	Breed	Age (Years)	History
Alex	Small	Male	Y	6	14	Poodle Mix	2	Stray
Bella	Large	Female	N	18	40	Boxer / Black Mouth Cur	3	Stray
Bosco	Large	Male	N	24	53	Terrier mix	3	Stray
Bruno	Small	Male	Y	7	15	Norfolk Terrier	3	Return
Chancet	Small	Female	Y	3	6	Poodle mix	10	Stray
Chico	Small	Male	Y	5	11	Miniature Pinscher / Chihuahua mix	2	Return
Chloe	Small	Female	Y	9	19	Terrier mix	1	Transfer In
Dottie	Small	Female	Y	5	12	Terrier mix	3	Return
Dumpling	Small	Female	N	6	14	Dachshund	4	Stray
Eddie	Small	Male	N	8	17	Miniature Pinscher / Jack Russel Terrier mix	2	Found
Fester	Small	Male	Y	8	18	Terrier mix	5	Stray
Grace	Small	Female	Y	8	18	Miniature Pinscher mix	5	Owner Surrender
Homer	Small	Male	Y	5	11	Chihuahua mix	7	Stray
Liberty	Large	Female	Y	28	61	Terrier mix	1	Owner Surrender
Lil Moma	Small	Female	Y	7	15	Shih Tzu	5	Owner Surrender
Markus	Large	Male	Y	19	41	Hound mix	2	Stray
Max	Small	Male	N	4	9	Chihuahua mix	2	Stray
Miss Lady	Large	Female	Y	32	70	Labrador Retriever	8	Stray
Missy	Small	Female	Y	6	14	Terrier mix	2	Owner Surrender
Mitzi	Small	Female	Y	7	16	American Eskimo	5	Owner Surrender
Nelson	Large	Male	Y	34	74	Retriever mix	1	Owner Surrender
Peanut	Small	Male	Y	7	15	Terrier mix	6	Owner surrender
Poley	Large	Female	N	19	42	Terrier mix	4	Stray
Precious*	Large	Female	Y	25	54	Pit Bull Terrier mix	6	Abandoned
Snow*	Large	Female	Y	23	50	Pit Bull Terrier mix	2	Return
Scooter	Large	Male	Y	19	42	Border Collie/ Retriever mix	2	Stray
Rocko*	Large	Male	Y	20	45	Shepherd mix	3	Stray
Tucker*	Large	Male	Y	21	47	German Shepherd mix	2	Stray
Shy	Small	Female	N	6	13	Terrier mix	1	Stray
Simmy	Small	Male	Y	5	11	Chihuahua / Dachshund mix	4	Stray
Stud	Large	Male	N	21	47	Bulldog	5	Owner Surrender
Tasha	Large	Female	N	20	43	Australian Cattle Dog mix	2	Stray

Table 1 (continued).

| Name	Size	Sex	Altered	Weight (kg)	Weight (lbs)	Breed	Age (Years)	History
Tiara	Large	Female	Y	20	43	American Blue Heeler mix	3	Stray
Thurston*	Large	Male	Y	24	53	Pit Bull Terrier mix	2	Stray
Tig*	Large	Male	Y	29	63	Pit Bull Terrier mix	2	Owner Surrender
Tabbie	Large	Female	N	20	43	Pit Bull Terrier mix	2	Transfer In
Trip	Large	Male	N	33	72	Mastiff mix	1	Owner Surrender
Vixen	Large	Female	N	22	49	Labrador Retriever mix	5	Abandoned
Zena	Small	Female	Y	8	17	Boston Terrier mix	1	Stray

* Asterisks in succession indicate matched subjects.

For each subject, the weight, color, spay/neuter status and estimated age and breed type, were recorded along previous history r (i.e. owner surrender, stray, or another condition). Only dogs that were deemed adoptable by the HSSM, dogs that were healthy and non-aggressive to humans, were chosen for participation. In addition, dogs that appeared to have behavioral issues, such as hyperactivity, or sensory impairments were not used in this study. These characteristics were assessed during the training phase described below. While specific details about the history of most individuals, including their previous interactions with humans, was not available, these and other individual differences are compensated for statistically by the large sample size. Utilizing a large sample size aided in discerning patterns between groups across a wide range of histories and physical characteristics.

Procedure

Animals were tested in a room approximately 3 x 4 m in size. The participant was held on one side of the room by an assistant while the experimenter and platform was stationed on the other side of the room facing the participant (Figure 1). The platform

consisted of a large mat approximately 1 x 0.5 m in size. Dogs were stationed with no more than 1.5 m for large dogs and no more than 1 m for small dogs between the participant and the platform. Opaque Dixie© or Solo© cups were used as occluder containers. Occluder cups for large dogs were 10×8.3 cm in height and cups for small dogs were 7.5 cm x 10 cm in height. Occluder cups for extremely small dogs, 2.2 kg (5 lbs) and under, were 5.5 cm x 6 cm in height. To control for olfactory cues, small pieces of the food rewards were placed in between two cups which were secured together with clear tape. The top cup was altered to have several small air holes so the scent could escape. Occluder cups were placed on the platform at least 30 cm apart.
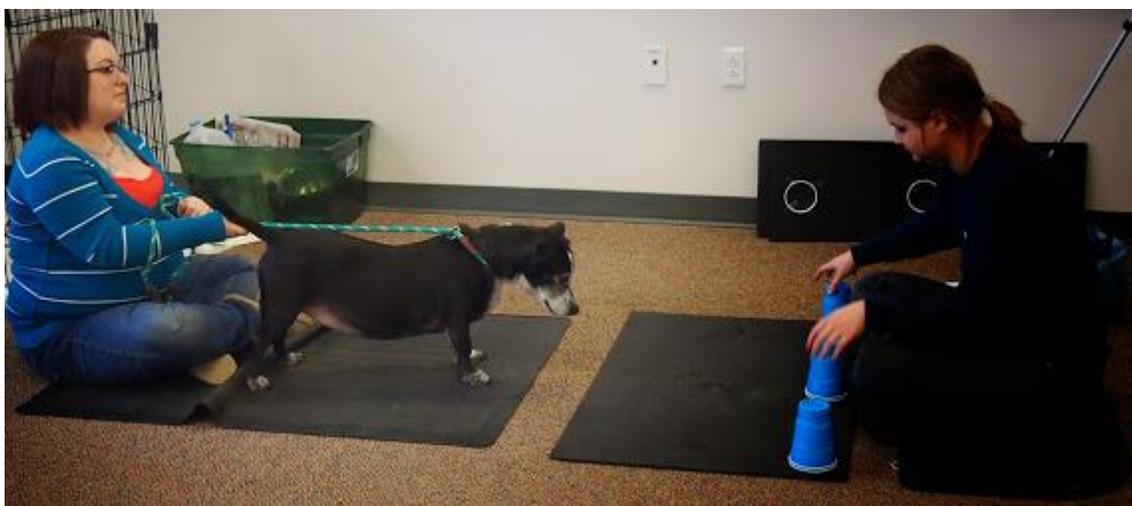
Figure 1. Experimental arrangement.

Throughout testing, the first occluder that a participant touched with its nose or paw was considered its choice for each trial. The Numbers© spreadsheet application was used to record participant responses on an iPad©. When the participant indicated a correct choice the participant was allowed to consume the reward. When a participant chose incorrectly the experimenter showed the dog the reward in the correct location after each trial but the dog was typically not allowed to consume the reward. Small treats, which

were desirable food items, were used as rewards for all tasks. Depending on the participants' motivation and the demands of the various tasks, occasional food rewards were provided in between trials to maintain the participant's motivation and attention. Sessions were videotaped with an HD digital video camera located behind the experimental platform. Testing was suspended for a participant whenever the animal seemed to no longer be motivated by the food reward, such as when the participant's attention could not be gained by the experimenter.

Training Trials

Acclimation. The dog was brought into the testing area and was free to roam around the room while up to three experimenters sat down around the perimeter of the room. For dogs that appeared to be timid or were likely to avoid contact with the occluder cups, several small treats were placed on the platform uncovered, inside cups that were on their side, or under cups. Experimenters did not speak to or direct attention toward the dog during this time unless the dog approached. When this happened, experimenters would pet the dog briefly and then stop to encourage continued exploration of the room. The acclimation period ended when the dog found and ate all of the treats and showed no apprehension around the cups.

One Cup Training Trials. A piece of food was placed on the platform and then covered by an occluder cup while the participant was watching. The participant was then released while still on leash and allowed to pursue the reward. Once the participant touched its nose, mouth, or paw to the occluder the experimenter verbally rewarded the participant and lifted the occluder to reveal the reward. This was repeated until, upon release, the participant approached and touched the occluder without hesitation.

Task Trials

Unless otherwise indicated, 10 trials from each of the following tasks were conducted for each participant. If a participant failed to complete all 13 tasks, another dog matching the general breed type, size, sex, and alternation status was selected to complete the remainder of the tasks.

Dogs were given a five minute break between every one to four task types and were walked outside for five to ten minutes at least once every 30 minutes. For participants that seemed unmotivated near the end of the previous task, a food motivation trial was conducted before beginning a new task. The motivation trial was simply a trial from one of the previous task types that the dog performed well on such as the one cup training task or the two cup one reward task.

For each task below, reward placement for each trial was presented in a predetermined, pseudo-random order; all trial locations were baited on a balanced schedule and no trial location was baited more than two times in a row. The order of occluder manipulation was also randomized to prevent cueing, placement bias, and problem solving via a global rule. To prevent cueing via eye gaze, experimenters refrained from looking at the occluders.

Task 1-3. Spatial Memory. The experimenter showed the participant the reward(s) and with the participant watching, placed the reward(s) on the platform in the predetermined location(s), then covered the reward(s) with the occluders which were placed in line approximately 30 cm apart. The participant was released while still on leash and allowed to make up to one choice for trials involving one reward, and up to two choices in succession for trials involving two rewards.

Task 1. Two cups, one baited: The reward was placed on either the right or left side of the platform and both locations were covered with occluder cups. The participant was given one chance to locate the reward. Correct choices received a score of 1 while incorrect choices received a score of 0.

Task 2. Three cups, one baited: The reward was placed in the right, center, or left position, and then all locations were covered with occluders. The participant was given one chance to locate the reward. Correct choices received a score of 1 while incorrect choices received a score of 0.

Task 3. Three cups, two baited: Rewards were placed in two of the three positions on the platform (right, center, or left) then all locations were covered with occluders. After the participant made the first choice and obtained the reward, the assistant briefly tugged on the leash for less than 1 second to distract the dog from commencing general search behavior. The participant was then allowed to make a second choice. If the participant chose the empty container, then no other choices were allowed. If the participant chose correctly the first time but not the second time, it received a score of 0.5. If the participant chose correctly both times it received a score of 1.

Task 4-6. Object Permanence. The experimenter placed three occluders on the platform in a row. Each occluder was placed approximately 30 cm apart. Then experimenter placed the reward to the left of center on the platform and , with the participant watching, covered it with the displacement device, a small opaque container approximately 1/3 the height of the occluder cups. The occluders were them manipulated in one of three possible ways.

Task 4.   Single displacement: The experimenter tilted the target occluder forward

and slid displacement device containing the reward under the occluder. The

displacement device was removed and the occluder was replaced. The reward

was left under the occluder. The other occluders were not manipulated.

Task 5.   Double adjacent displacement: The experimenter tilted one occluder

forward and slid the displacement device containing the reward under this

occluder. Without lifting the displacement device, the displacement device was

slid under a second adjacent occluder where the reward was deposited. The

displacement device was removed leaving all three occluders in a row. The

remaining occluder was not manipulated

Task 6.   Double non-adjacent displacement: The experimenter tilted either the right

or left occluder forward and slid the displacement device containing the reward

under this occluder. Without lifting the displacement device, the displacement

device was slid under the second non-adjacent occluder where the reward was

deposited. The displacement device was removed leaving all three occluders in a

row. The center occluder was not manipulated

After depositing the reward under the occluder, the experimenter showed the

participant that the displacement device was empty. The displacement device was then

hidden out of sight. For single displacements the participant was allowed to make one

choice and for double displacements the participant was allowed to make two choices

while still on leash. The trial was ended when the participant either located the reward or

touched on occluder that had not been manipulated. For single displacement trials,

participants had to choose the occluder that was manipulated by the experimenter before

choosing any occluder which was not manipulated. Correct responses received a score of

1. For double displacement trials, participants were required to choose either the baited

occluder or both the baited occluder and the other occluder that was manipulated by the

experimenter in order to receive a score of 1. If the participant chose the un-baited

manipulated occluder followed by an un-manipulated, occluder it received a score of 0.5.

Task 7-9: Rotation. The experimenter showed the participant the reward and then

with the participant watching, placed it on a testing platform in the predetermined

location. Three occluders were aligned in a row approximately 30 cm apart on the

platform so that one of the occluders covered the reward. The experimenter performed

one of three possible rotations after which the participant was given one chance to locate

the reward.

Task 7.   360° side: The reward was placed on the platform in either the right or left

position and three occluders were placed in a row covering the reward. The entire

platform was rotated clockwise 360° so that the reward ended in the same position

in which it started.

Task 8.   180° center: The reward was placed on the platform in the center position

and three occluders were placed in a row covering the reward. The entire platform

was rotated clockwise 180°; thus, the reward ended in the same position in which

it started. For this task, only 5 trials were performed.

Task 9.   180° side: The reward was placed on the platform in either the right or left

position and three occluders were placed in a row covering the reward. The entire

platform was rotated clockwise 180° so that the reward ended in the opposite

position in which it started.

While still on leash, the participant was allowed to choose one location. Participants had to choose the baited location to receive a score of 1.

Task 10-13. Transposition. The experimenter showed the participant the reward, then with the participant watching, placed it on a testing platform in the predetermined location. Three occluders were aligned in a row approximately 30 cm apart so that one of the occluders covered the reward. The experimenter performed one of four possible transpositions after which the participant was given one chance to locate the reward.

Task 10.   Single non-baited transposition: The experimenter transposed two non-baited occluders without touching the baited occluder.

Task 11.   Single baited transposition: The experimenter transposed the baited occluder with one of the empty occluders without touching the third occluder.

Task 12.   Double non-baited transposition: The experimenter transposed the two empty occluders and also transposed the baited occluder with one of the empty occluders.

Task 13.   Double baited transposition: The experimenter transposed the baited occluder with one of the empty occluders, and then transposed the baited occluder again with one of the empty occluders.

While still on leash, the participant was allowed to choose one location. Participants had to choose the baited location to receive a score of 1.

Data Analysis

Assumptions

MANCOVA. A MANCOVA analysis was found to be appropriate as the crucial assumptions for the analysis were met. All data sets were independent with random sampling. The dependent variables were not highly positively correlated with one another as no correlations were higher than $r = 0.3$. Multivariate normality was assessed by looking for large gaps in Mahalanobis distance calculations. Only one value was found to differ greatly from the others with a score of 0.23, compared to the next closest score of 1.10. Removing, this record did not change the results of the omnibus tests for the MANCOVA; therefore this record was not excluded from the analysis. The data appeared to be near normal with pseudo-z scores for skewness and kurtosis not exceeding three. Box's M and F-Max tests were non-significant indicating homogeneity of covariance matrices. An ANOVA comparing the independent variables sex and size, to the covariate altered, was non-significant meaning the covariate and treatment effect were independent. Overall, there was homogeneity of regression slopes except for the three way interaction between the covariate and both independent variables which was nearing significance for displacement, $F(1,31) = 4.055$, $p = .054$.

One Sample t-Tests. One sample t-tests were conducted to compare the scores of males and females to chance levels of performance. In all, 19 females and 17 males were included in the analysis. The data appeared to be near normal with pseudo-z scores for skewness and kurtosis not exceeding three.

Calculations for Chance Levels of Performance

Calculations for Each Task Type: Calculations for level of chance performance varied according to task type. The majority of tasks involved trials with only one choice. For trials where dogs had only one choice to locate the reward, there were three possible locations, and dogs could earn either 1 point or 0 points. Dogs should have been able to locate the treat 33.3333% of the time, or one out of every three trials, just by guessing for a total score of 3.3333 for a 10 trial task.

On some tasks, dogs were given up to two chances to locate the reward in two different rounds. There were two variations of these tasks: the three cups, two baited task (Task 3), and the double displacement tasks (Tasks 4 and 5). For Task 3, on the first round, there were three possible locations with two of the locations baited with treats. In the first round, participants would score a 0.5 (by choosing one of the two possible options) by chance on two thirds of 10 trials, or 66.6667% of the trials. This means that on 6.6667 trials dogs would go on to the next round by chance. In the second round there were only two locations to from which to choose. Consequently, on half of these trials, (3.3333 trials), a correct choice by pure chance would earn the participant another 0.5 points. Therefore, to determine the score that could be attained by chance: on round one, participants would score a 0.5 on 6.667 trials, for a total of 3.333; and for the second round, they would score an additional 0.5 on 3.333 trials, for a total of 1.667. Adding the 3.3333 points for the first round and 1.6667 points in the second round resulted in a total chance score of 5 points on this task.

Tasks 4 and 5 differed in that, in the first round there were three possible locations, and two of the locations were considered correct even though the treat was

located in only one of the locations. On this round, dogs could score a 1 on one third of the trials if they found the treat on the first try, or they could also score a 0.5 on one third of the trials if they chose the non-baited correct location. If the dog scored 0.5 on the first round, they were given a second chance to locate the treat, but this time there were only two possible locations remaining. This means they had a 50/50 chance of finding the treat on one third of these second round trials, 1.6667 trials in total. If dogs chose correctly on these trials, they would earn 0.5 points per trial for a total of 0.8333 points. In summary, by chance alone dogs could score a 1 on one third of trials (3.3333 points), on another one third of trials they could score 0.5 (1.6667 points), and then in the second round on one half of the 3.333 trials they could score a 0.5 (0.83333 points). Therefore, dogs could score 5.8333 points by chance on double displacement tasks.

Calculations for Task Sets: For spatial memory, there were three tasks with 10 trials per task for a total of 30 trials. On Task 1, dogs were given once chance to locate the reward with only two possible locations for a chance score of 5 points. For Task 2, dogs were given only one chance to choose the correct location out of three possible locations and could earn 3.3333 points per task by chance alone. The third task was the three cups two rewards task described previously where dogs could earn 5 points by chance. In total, dogs could score 13.3333 points by chance on the spatial memory set.

There were three displacement tasks with 10 trials in each task. On one of the tasks, dogs were given only one chance to choose the correct location and could earn 3.3333 points by guessing. In the remaining displacement tasks dogs were given up to two chances to locate the reward and could earn 5.8333 points per task by chance alone. For the displacement task set the total score dogs could earn by guessing was 14.9933.

In all, there were three rotation tasks, one with five trials and two with 10 trials each for a total of 25 trials. With each trial, the dog had three locations to choose from and dogs were only given one chance to find the reward. For tasks with 10 trials, dogs could earn 3.3333 points by just guessing, and for the task with only five trials, dogs could earn 1.6667 points by guessing. On this task set, dogs could earn a total of 8.3333 points by chance alone.

For transposition, there were four tasks with 10 trials in each task. Each trial presented the dog with three possible locations from which the dogs were allowed to choose. On each task, dogs could score 3.3333 points by chance alone for a total score of 13.3333.

A total of 13 different tasks were tested for each subject. Each task type consisted of 10 trials, with the exception of one task (Task 8), which had only five trials. Scores for each subject were consolidated (summed) into four major categories: Spatial Memory (3 tasks, 30 trials total), Displacement (3 tasks, 30 trials total), Rotation (3 tasks, 25 trials total), and Transposition (4 tasks, 40 trials total). These categories were determined sufficient because no significant differences in size or sex were detected in a 2 x 2 MANOVA that included all tasks as 13 dependent variables.

CHAPTER III

RESULTS

MANCOVA

The variable 'altered' which refers to spay/neuter status was added as a covariate in a 2 x 2 MANCOVA with four dependent variables. According to the MANCOVA omnibus test there were no differences between large and small dogs (F (4,28) = 1.189, p = .337, η_p^2 = 0.145), however there was a significant relationship between the covariate 'altered' and the DV's, F (4,28) = 5.61, p = .002, η_p^2 = 0.445. There was also a main effect of sex (F (4,28) = 6.09, p = .001, η_p^2 = 0.465) but no other differences were found. Contrasts showed that there were differences in sex for spatial memory ($F(1,31)$ = 4.526, p = .041, η_p^2 = 0.127) and transposition, $F(1,31)$ = 9.944, p = .004, η_p^2 = 0.243. For spatial memory females performed better than males and for transposition males performed better than females (Figure 2). To determine whether these performances differed from chance, post-hoc one-way t-tests were performed.

Comparisons to Chance Levels of Performance

Overall, dogs performed no different than chance levels on transposition tasks with a mean score of 12.94. However, when looking at males and females separately, females scored significantly below chance with a mean score of 11.95 ($t(18)$ = -2.433, p

= .026, d = -0.14) while males scored slightly above chance (M = 14.06), however, this

difference was not significant (Figure 2).
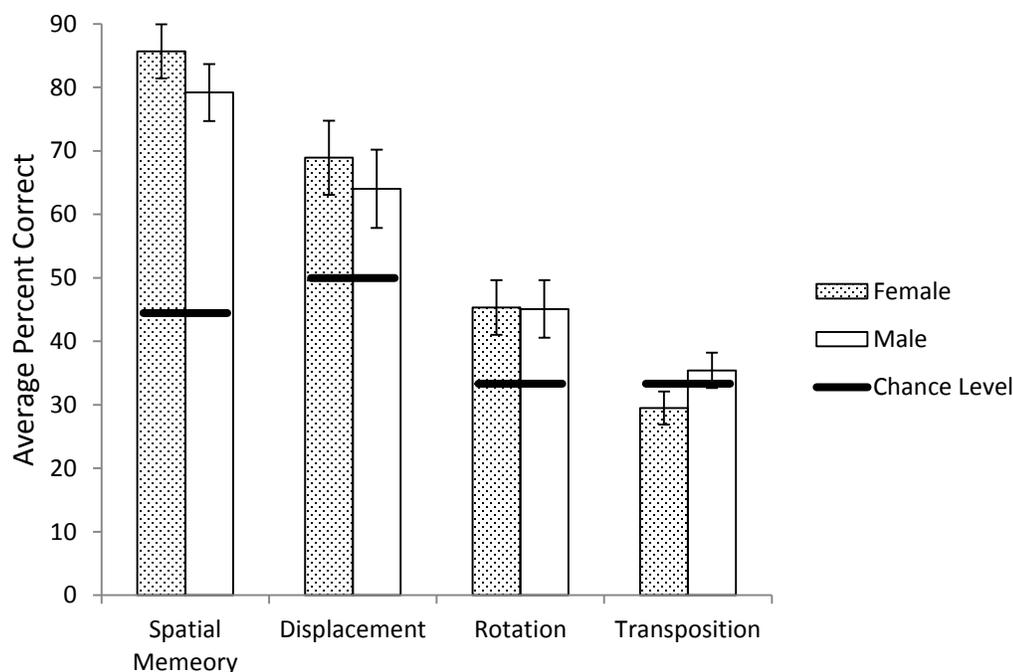
Figure 2. Mean scores of male and female dogs for the four task sets shown as percentage of correct responses. Black bars indicate chance levels of performance. Error bars are 95% confidence intervals.

To further investigate these differences, altered and unaltered status were

compared (Figure 3). On the transposition task set the average score of unaltered

individuals was 15.00 points, whereas the average score of altered individuals was 11.91.

Upon examining altered and unaltered males and females separately, the differences were

even greater. The average score of unaltered males was significantly above chance ($t(4)$ =

6.631, p = .003, d = 2.97) with a mean score of 17.20, and the mean score of altered

females was significantly below chance ($t(11)$ = -3.426, p = .006, d = -0.99) with a mean

score of 11.08. The scores of altered males (M=12.75) and unaltered females (M=13.43)

were no different than chance (altered males $t(11) = -0.849$, $p = .414$, $d = -0.25$; unaltered females $t(6) = 0.113$, $p = .914$, $d = 0.04$).
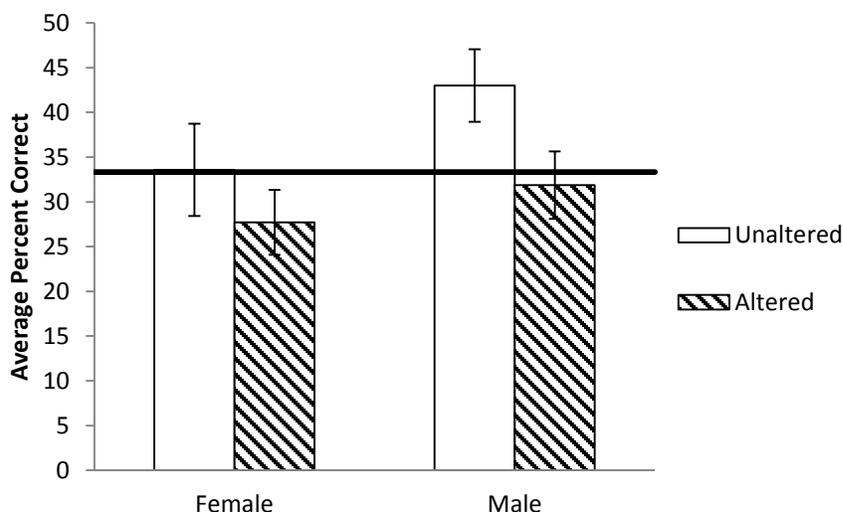
Figure 3. Average scores of male and female altered and unaltered dogs for the transposition task set shown as percentage of correct responses. Black bar indicates chance level of performance. Error bars are 95% confidence intervals.

For spatial memory, displacement, and rotation dogs, including males and females separately, scored significantly above chance (spatial memory $t(35) = 24.12$, $p < .001$, $d = 4.02$; displacement $t(35) = 7.97$, $p < .001$, $d = 1.33$; rotation $t(35) = 7.97$, $p < .001$, $d = 1.33$) (Figure 2). Dogs do not typically perform well on rotation tasks, so separate analyses were conducted for each of the three rotation tasks (Figure 4). Dogs were able to perform well on the 180° center rotation task ($t(35) = 14.95$, $p < .001$, $d = 2.36$) and the 360° rotation task ($t(35) = 10.42$, $p < .001$, $d = 1.65$) where, after manipulation, the reward ended in the same location where it began. Dogs performed significantly below chance on the 180° side task ($t(35) = -16.35$, $p < .001$, $d = -2.58$) where the platform was rotated 180 degrees with the treat located on the right or left location. In this task, after

manipulation, the treat ended in a different location than where it began. The trends

described above were the same for males and females separately.
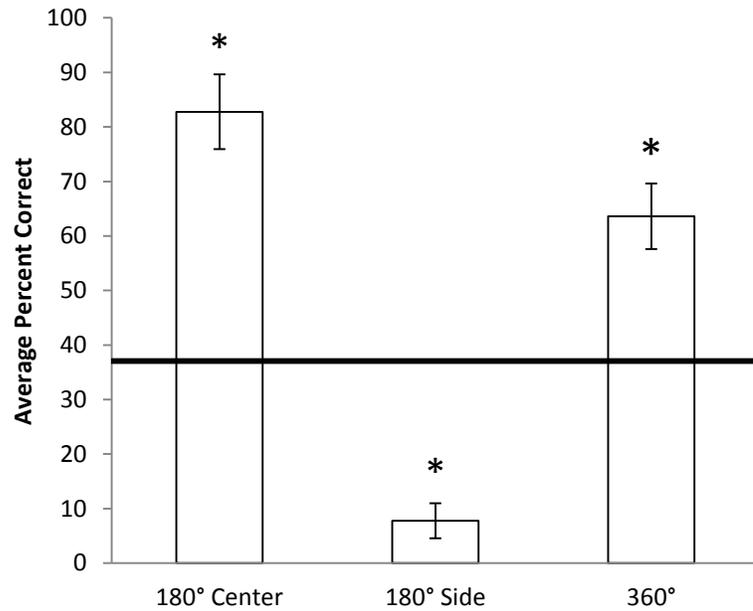
Figure 4. Mean scores for rotation tasks shown as percentage of correct responses. Black
bar indicates chance levels of performance. Error bars are 95% confidence intervals.
Asterisks indicate a significant difference from chance level of performance.

CHAPTER IV

DISCUSSION

Does Size Matter?

In contrast to previous findings on a social cognition task by Helton and Helton (2010), large and small dogs performed similarly across spatial cognition tasks, despite differences in size. Helton and Helton (2010) suggested that inter-ocular distance could be responsible for the higher performance of large dogs. In this study, inter-ocular distance was controlled for through the categorical size differential. However, this was inconsequential because differences due to size were not detected.

Differences in inter-ocular spacing are inherent when comparing large and small dogs, but if this were the reason for the superior performance of large dogs in the Helton and Helton (2010) study, then large dogs should outperform small dogs on all types of cognitive tasks. Since large dogs and small dogs performed equally on spatial tasks, it is unlikely that inter-ocular spacing is responsible for the differences observed by Helton and Helton (2010).

Another possibility is that large dogs have an innate capacity to communicate better with humans due to breeding history, but this difference is not evident in non-communicative tasks, such as the spatial memory tasks tested here. This mirrors the domestication hypothesis which claims that dogs are superior to wolves in their ability to communicate with humans based on genetics, regardless of experience (Hare et al., 2002). However, several studies have shown that dogs and wolves perform equally on social tasks when the wolves have had extensive enculturation (Gácsi, Gyoöri, et al., 2009; Miklósi et al., 2003; Udell et al., 2008; Virányi et al., 2008). If there are no differences in social cognition between wolves and dogs, which are separated by

thousands of years of breeding, then it is unlikely that there would be major differences in social cognition within either species. Still, genetic disposition cannot be ruled out as a factor in social cognition. It may be that genetic traits other than an innate ability to understand human communicative cues are responsible for differences in performance on social tasks. These could include differences in learning ability, attention, inhibition, motivation, dominant sensory modality, and temperament.

The most supported explanation is that differences in communicative ability found within dogs as a species are due to differences in enculturation. This would explain why wolves that have had undergone intensive enculturation perform on par with dogs. In addition, there is some evidence that dogs raised with minimal human contact perform poorly on the object choice task (Lazarowski & Dorman, 2015; Udell, Dorey, & Wynne, 2010). Previous experience with humans matters much less in spatial tasks because in these tasks all dogs receive the same training in a novel situation, whereas social tasks utilize communicative cues that almost all dogs have encountered before, some more extensively than others. If large dogs receive more training and interaction with human communicative cues than small dogs, this difference could be the reason they perform better than small dogs on social tasks. Future research should seek to control for prior experience with humans in order to determine if enculturation has an effect on the performance of large and small dogs.

<div align="center">Sex and Alteration Status</div>

Although size was not found to have a significant effect on performance, sex and altered status had an effect for two task types: spatial memory and transposition. Both males and females performed above chance on the spatial memory task set, but females

score significantly higher than males. One possibility for the higher performance of females is that this was the first set of tasks in the series, and it is possible that females were able to become acclimated to the testing environment more quickly than males. This would have allowed them to focus more on the tasks resulting in a higher overall score.

In contrast, neither males nor females scored significantly above chance in the transposition trials. Males scored no different than chance indicating they were purely guessing while females unexpectedly scored significantly below chance, indicating that they may have been using a different search strategy than males. One strategy that could have resulted in poorer performance would be to search in the location where the reward was last seen. The first transposition task of the four could be solved using this strategy but the three subsequent tasks could not be solved in this way. If females continued to use the same strategy in all four transposition tasks, this would have resulted in below chance performance as they would not have been able to locate the reward in three fourths or 25% of the trials. However, females scored somewhat better than this with an average score of 11.95 or 29.88% indicating that at least some females did not use the same strategy throughout. In addition, males may have been faster to abandon a nonworking strategy in favor of a random or fixed pattern of guessing. This could indicate that males are more inclined to take risks whereas females are more reluctant to adopt a new strategy.

The effect of alteration status may have also played an important role in the type of search strategy used. Alteration seemed to impact the performance of males but not females. Altered and unaltered females had similar scores and the performance of unaltered males was comparable to females. In contrast, altered males scored much

higher than the other groups with scores at levels near chance. Although the disparities found for sex and alteration status are interesting, these were small and may not be indicative of true cognitive or behavioral differences.

Whether there are actual cognitive differences between male and female dogs remains to be seen. Very few studies have investigated sex differences in dogs and the results have been inconsistent. Müller et al., (2011) found that females performed better than males in a size consistency violation task but found no sex differences in a later study utilizing variations of the Piagetian invisible displacement task (Müller et al., 2014). One other study found inverse effects within the same task (Duranton et al., 2015). Males performed better in the initial phase of the task and females performed better in the final phase. If sex differences do exist, it may be that they are due to an underlying factor such as attention or temperament that affects behavior and performance on cognitive tests.

<div align="center">General Findings</div>

Dogs performed better than expected on several task types based on comparisons to chance levels of performance. The dogs did well on the spatial memory tasks and did poorly on transposition tasks supporting the findings of multiple studies (Doré et al., 1996; Fiset et al., 2000; Fiset & Plourde, 2013; Gagnon & Doré, 1992, 1993, 1994; Rooijakkers et al., 2009; Triana & Pasnak, 1981). However, the higher performance on displacement tasks and the rotation task set was not expected. Upon further investigation, these findings could be explained in terms of biases in search patterns.

In earlier studies, dogs were successful at solving Piagetian invisible displacement tasks (Gagnon & Doré, 1992, 1993, 1994; Triana & Pasnak, 1981), but more recent work

has made the claim that they cannot solve this task unless final resting position of the displacement device is adjacent to the target location (Collier-Baker et al., 2004; Fiset & Leblanc, 2007). This claim was supported in part because in one study, dogs could no longer solve the task when the displacement device was removed (Collier-Baker et al., 2004). However, in the removal condition, the displacement device was never actually removed. Instead, the experimenter hung the device on a wall behind a curtain, a time-consuming process that may have increased the saliency of the device itself. In fact, many dogs went behind the curtain to stare at the device which hung out of reach.

The use of a displacement device in general has been shown to negatively impact performance on visible displacement tasks which dogs are capable of solving (Müller et al., 2014). The increased saliency of the displacement device used in invisible displacement tasks may be the cause of these conflicting reports and may result in poorer performance to some degree (Müller et al., 2014). While conducting the current study, the displacement device was covertly hidden after each manipulation. Because its resting position was not visible, the dogs were less likely to be negatively influenced by the use of the device while searching for the reward.

Contrary to other studies, initial analysis with all three rotation tasks combined showed that dogs were able to do well on this type of invisible displacement task. However, when looking at the three tasks separately, dogs performed well above chance on the 360° and 180° center rotation tasks but performed below chance on the 180° side task as expected. Both the 360° and 180° center tasks could be solved by following the rule "search the location where the target was last seen" which is also the initial location of the target. Dogs tend to first search in the target's initial location (Doré et al., 1996;

Fiset & Plourde, 2013; Miller et al., 2009; Plourde & Fiset, 2013) and, of the three tasks, the 180° side task is the only rotation task that could not be solved by searching the initial location. These results are consistent with other studies that found that dogs do not perform above chance on the standard 180° side rotation task (Fiset, 2007; Miller et al., 2009).

Conclusion

The evidence presented here suggests that size does not affect performance on spatial cognition tasks. Therefore, it is unlikely that differences found in social tasks are due to physical factors related to size, such as binocular vision or inter-ocular distance; although other physical factors such as skull shape could play a role as these factors were not controlled for in this study. Further investigation is needed to determine why other researchers have found differences in the performance of large and small dogs on social tasks. Canine research that involves social cognition or depends on reading human communicative cues should control for size, sex, and other variables that may affect performance. Genetic differences in basic cognitive traits such as motivation, attention, and inhibition may be important, but enculturation has also been shown to affect performance on social tasks. Researchers should carefully consider previous experience when drawing comparisons within and between species.

APPENDIX A

IACUC APPROVAL

**THE UNIVERSITY OF SOUTHERN MISSISSIPPI.**

INSTITUTIONAL ANIMAL CARE AND USE COMMITTEE
118 College Drive #5116 | Hattiesburg, MS 39406-0001
Phone: 601.266.4063 | Fax: 601.266.4377 | iacuc@usm.edu | www.usm.edu/iacuc

INSTITUTIONAL ANIMAL CARE AND USE COMMITTEE NOTICE OF COMMITTEE ACTION

The proposal noted below was reviewed and approved by The University of Southern Mississippi Institutional Animal Care and Use Committee (IACUC) in accordance with regulations by the United States Department of Agriculture and the Public Health Service Office of Laboratory Animal Welfare. The project expiration date is noted below. If for some reason the project is not completed by the end of the three year approval period, your protocol must be reactivated (a new protocol must be submitted and approved) before further work involving the use of animals can be done.

Any significant changes (see attached) should be brought to the attention of the committee at the earliest possible time. If you should have any questions, please contact me.

PROTOCOL NUMBER: **13101703**
PROJECT TITLE: **A Survey of Cognition in Dogs and Cats**
PROPOSED PROJECT DATES: **9/2013 – 9/ 2015**
PROJECT TYPE: **New**
PRINCIPAL INVESTIGATOR(S): **Heidi Lyn**
DEPARTMENT: **Psychology**
FUNDING AGENCY/SPONSOR:
IACUC COMMITTEE ACTION: **Full Committee Approval**
PROTOCOL EXPIRATON DATE: **September 30, 2015**
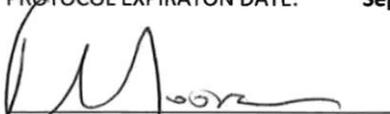
_____   10 ~15 ~13
Frank Moore, Ph.D.   Date
IACUC Chair

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