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Time, Number, Space, and the Domestic Dog

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ABSTRACT

Over the past 20 years, the field of animal cognition has seen a dramatic increase in the attention given to the study of cognition in the domestic dog. Since their origin at least 10, 000 years ago, dogs have been artificially selected by humans to protect our homes, guard our livestock, pull our sleds, and a multitude of other functions. Given their close relationship with humans, much of the current research in the area of dog cognition to date has focused on aspects of social cognition. Considerably less attention has been paid to domains that have traditionally been areas of heavy focus in the animal cognition literature. This dissertation focuses on three areas, which are addressed as "fundamental" aspects of cognition—namely, numerical discrimination, interval timing, and spatial memory. These areas were chosen because a.) they are basic processes fundamental to the daily existence of an animal in the wild, and b.) because these topics have been studied rigorously in traditional animal cognition research, yet have received little attention in the area of dog cognition.

In the first set of studies, a numerical discrimination task using sequential presentation of stimuli was used, in which subjects watched as a different number of food items were dropped into each of two bowls. The subjects were then allowed to select and consume the contents of one of the bowls. Although dogs excelled in a 1 vs 0 condition, their performance did not significantly surpass chance across all other ratios. In a second experiment with a single subject, a simultaneous task was used in which stimuli were presented on two magnet boards. Using this simultaneous presentation, ratio effects consistent with both Weber's Law and the Approximate Number System were demonstrated.

In the second set of studies, interval timing was demonstrated using a fixed interval

30-s schedule, with either a light or a tone + light compound signalling the beginning of each fixed interval. When dogs in the compound group were subsequently tested with 60-s tone-only probe trials, the dogs' rate of responding peaked near 30 s. When the same dogs were tested with light-only probes, however, no evidence of timing was found, revealing an overshadowing effect of tone over light. In a second experiment, a bi-section task was used in which dogs had to learn to approach one feeder when given an 8-s tone + light signal, and another feeder when given a 2-s tone + light signal. When subsequently tested at intermediate durations, psychophysical curves again showed clear control of timing by the tone stimulus but not by the light stimulus.

The final set of studies were an attempt to investigate both reference and working memory, within a spatial memory task. A win/shift design was used, in which dogs searched for food within the four corners of a large area (an empty classroom in Experiment 1, and an outdoor field in Experiment 2). Food items were hidden under plastic flower pots, which the dogs had previously been trained to knock over. The dogs' performance in locating rewards hidden consitently in the same location during the test phase (reference memory), was compared to their performance for locating rewards hidden in a different randomly-selected location from trial to trial (working memory). Dogs' performance varied across subjects, and implications of these individual differences are discussed.

Co-Authorship Statement

Chapters 2 and 3 are separately published as papers with myself (Krista Macpherson) as first author and Dr. William A. Roberts as co-author. I independently designed and performed the experiments described in all chapters of this dissertation, and wrote the papers as presented herein. Dr. William A. Roberts was consulted on best methods for designing the experiments and edited the papers. Copyright licenses for both of the published chapters are included in Appendix B.

Acknowledgments

At the beginning of the fourth year of my undergraduate training, I needed to find a thesis supervisor. Most students had already found one--but I was very shy, and had been terrified to talk to any faculty members about working in their labs. So I made an appointment to go talk to the professor running the thesis course that year about my predicament—I will forever be grateful that the professor in question was Dr. Bill Roberts. From our first meeting, Bill gave me the freedom to pursue a project that was less than conventional, all the while teaching me to examine an oft-anthropomorphized species through a critical and scientific eye. Having been Bill's student for over a decade now, I have come to know him not only as an outstanding researcher, but also as a kind and considerate human being. I have had few role models in my life, and I consider myself fortunate that he has been one of them.

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Chapter 1

General Introduction to Canine Cognition

The domestic dog (*Canis lupus familiaris*) has had an unusual history in psychological research.   Two historical giants—Darwin and Pavlov-- took great interest in the domestic dog. Darwin's observations, along with those of his one-time research assistant Romanes, however, were almost exclusively anecdotal. Pavlov's discovery of classical conditioning, on the other hand, was a serendipitous observation made while doing unrelated work on the digestive system. In spite of this early research with dogs, they were largely considered an "artificial" species due to their domestication (Miklósi, 2015) and were largely ignored in psychological research. The past two decades, however, have seen the rise of the domestic dog as a new "darling" in animal cognition research (Morell, 2009).

Theories of Domestication of the Domestic Dog

Why has intense interest recently been focused on dog cognition? Much of this interest seems to center around what has become known as the Domestication Hypothesis (Hare, Brown, Williamson, & Tomasello, 2002; Hare & Tomasello, 2005). Dogs descended from gray wolves (*Canis lupus)* at least 10, 000 years ago (Pollinger et al., 2010). There is an ongoing debate as to the precise date of domestication, however, with some researchers (Lindblad-Toh, 2005) claiming that domestication took place as early as 100,000 years ago. The domestication hypothesis holds that dogs more or less "self-domesticated" from their ancestor, the gray wolf. Early humans formed camps, from which they would discard various types of debris, including scraps of food. Wolves who were overly fearful or aggressive would not approach these camps--more docile wolves, however, could approach the humans to exploit this easy food source. These docile wolves were more successful from an evolutionary perspective and remained in the gene pool, ultimately becoming the domestic dog. During much of this period, they were in the company of humans, who eventually

selectively bred them for work, protection and companionship. As a result of this selective breeding, dogs are now an incredibly diverse species, consisting of hundreds of breeds of different size, shape, temperament, and function. Given this unique relationship with humans, dogs are thought to have acquired many human-like traits, including communicative, social, cooperative, and attachment behaviours.

Perhaps the most compelling support for the Domestication Hypothesis is rooted in the Russian politics of the Stalin era. Farmed silver foxes (*Vulpes vulpes*) have been selected in Russia for over 40 generations for non-aggressive behaviour towards humans, resulting in animals that are docile, friendly and as skilled as dogs in interacting with people. These foxes also show developmental, morphological and neurochemical changes consistent with those observed in other domestic animals (Trut, Plyusnina, & Oskina, 2003; Hare et al., 2005). The history of this fox project is a long and intriguing one. Dmitri K. Belyaev, a Russian scientist, hypothesized that the anatomical and physiological changes seen in domesticated animals could have been the result of selection on the basis of behavioral traits. More specifically, he believed that tameness was the critical factor in domestication. Belyaev wondered if selecting for tameness and against aggression would result in hormonal and neurochemical changes. Those hormonal and chemical changes could then be implicated in anatomy and physiology. This could mean that the anatomical differences in domesticated dogs were related to the genetic changes underlying the behavioral temperament for which they were selected.

Belyaev believed that he could investigate his questions about domestication by attempting to domesticate wild foxes, another member of the canid family. Belyaev and his colleagues took wild silver foxes (a variant of the red fox) and bred them, with a strong

selection criterion for tameness. At this time in Stalinist Russia, however, Lysenkoism (a political campaign against genetics brought about by Trofim Lysenko in the late 1920's, which did not formally end until 1964) was state doctrine, and biologists were forbidden to carry out research related to these questions. By the mid to late 1930s, many geneticists were executed or sent to labor camps, including Belyaev's own brother, who was taken away in the middle of the night by the secret police, and executed without trial. In 1948, genetics was officially declared a pseudoscience, resulting in the firing of all geneticists from their jobs (Hare, 2013). Belyaev knew that he would need to proceed with caution in order to avoid his brother's fate. He therefore constructed a ruse, telling the Russian government that selecting the foxes for tameness was done in order to benefit the fur industry…making the foxes more easily and safely handled by furriers. For decades, this façade held up.

Belyaev's efforts were not in vain—within four generations, foxes selected for tameness began to exhibit physiological and behavioral changes. Physiological changes included the development of floppy ears (a trait possessed by only one animal in the wild, the elephant, as an adaptation to keep surrounding skin cool), curly tails, and piebald coat colouring. Behaviourally, the foxes began wagging their tails and barking, a vocalization that is rarely made by wild canids. Vixens also began to have more frequent breeding cycles, a trait more consistent with dogs (which typically cycle every 6 months) than wild canids (which typically cycle once a year). Behavioural data showed overwhelmingly that the foxes bred for tameness were more tolerant and even sought out the attention of humans, when compared to another strain of foxes which had not been selected for tameness (Coppinger & Coppinger, 2001). These foxes are still bred today, and have at times been sold as pets.

Many people who have owned or interacted with these foxes report them to be even more tame and docile than many breeds of dog.

The selection for tameness in silver foxes, a fellow canid species, provides compelling evidence for the domestication hypothesis in domestic dogs. Aside from their current ubiquity in human societies, domestic dogs are also interesting for the assessment of the influence of domestication on cognition and behavior, as unlike many other domesticated populations, the wild ancestor of the domestic dog, the wolf is available for study.

One of the first publications to receive widespread attention in the modern era of dog cognition was the work of Hare and Tomasello (1999). In this study, ten domestic dogs were exposed to two different social cues indicating the location of hidden food, each provided by both a human informant and a conspecific informant. When giving an enhancement cue, the informant approached the location where food was hidden and then stayed beside it. For a gaze and point cue, the informant stood between the two hiding locations and oriented their body and gaze toward the one in which food was hidden. Eight of the 10 subjects were above chance with two or more cues. These findings were followed up (Hare, Brown, Williamson, & Tomasello, 2002) with a study using an object choice task, in which an experimenter hid a piece of food in one of two opaque containers, and the subject, who did not see where the food was hidden, was allowed to choose only one of the containers. Before presenting the subject with the choice, the experimenter gave a communicative cue indicating the food's location, either by looking at, pointing to, tapping on, or placing a marker on the correct container. Whereas dogs readily used such cues, non-human primates tend to fail at this task no matter what type of cue is given. They cannot use the cue spontaneously, and typically only learn to use these cues after many trials (Itakura, Agnetta, Hare, & Tomasello, 1999;

Call, Agnetta, & Tomasello, 2000). Interestingly, Hare et al. found that wolves who were raised by humans, like non-human primates, do not spontaneously use human cues, and struggle to learn them, whereas domestic dog puppies only a few weeks old, even those that have had little human contact, use these cues readily. These findings support the Domestication Hypothesis, as they suggest that during the process of domestication, dogs have been selected for a set of social-cognitive abilities that enable them to communicate with humans in unique ways.

While the work of Brian Hare and colleagues gained momentum in the United States, research was simultaneously being conducted in Europe which also supported the domestication hypothesis. Adam Miklósi and his colleagues (Miklósi et al., 2003), for example, found that under more simple conditions (such as when a container was simply touched by a human to indicate the correct location of food) wolves could learn to use a human cue. Two of four wolves also successfully used proximal pointing to solve the task. However, none of the wolves in this study was initially successful on a more difficult distal point cue (where the human extremity is no closer than 50 cm from the target container), and after hundreds of trials, only one wolf could perform significantly above chance.

Other studies from the European labs have shown that domestic dogs are able to find hidden food by following pointing gestures made with different parts of the human body (Miklósi et al. 1998), and to beg for food preferentially from people who are able to see them (Gácsi, Miklósi, Varga, Topál, & Csányi, 2004). Similar to the Hare et al. (2002) study, Virányi et al. (2008) found that four-month-old dog pups outperformed wolf pups in following human pointing gestures. Even after months of training and many hundreds of trials of point-following, the wolves only attained the performance level of naïve dogs

(Virányi et al., 2008). These findings, along with those of Hare and Tomasello (1999, 2005), have led researchers to propose that dogs possess unique and advanced social cognitive skills in interacting with humans.

Dog cognition research during the late 1990's opened an ongoing discussion into the phylogenetic and ontogenetic processes by means of which dogs come to use social cues to locate food (Roberts & Macpherson, 2016). This debate continues today, and while the research described above favours a phylogenetic account (the Domestication Hypothesis), other researchers support an ontogenetic account of dog behavior. Udell, Dorey, and Wynne (2008), for example, showed that wolves, when highly socialized with humans, can use human pointing cues to find food without training, whereas dogs tested outdoors and dogs at an animal shelter (who would have limited contact with humans) do not follow the same human points. Udell et al. proposed that the reported failure of wolves in some studies may be due to differences in the testing environment, and concluded that domestication is not a prerequisite for human-like social cognition in canids, and that these skills are likely the result of conditioning that dog puppies receive from the time they start interacting with humans, typically at 8 weeks of age.

As a result of their findings, Udell, Dorey and Wynne (2010) subsequently outlined an alternative account to the domestication hypothesis. They provide substantial reasoning for the idea that the dogs' ability to interact with humans is the result of ontogeny, rather than phylogeny. Domestic dogs have much smaller brains than wolves, which has been attributed to developmental neoteny in dogs (Coppinger & Coppinger, 2001). Udell et al. posit that it is counterintuitive that reduction in brain size as a result of domestication would also be accompanied by an increase in social complexity. They further argue that since humans and

dogs are not conspecifics, it is unlikely that dogs could have an innate ability to exploit the behaviour of humans to their benefit in the absence of individual experience—rather, dogs must acquire these skills in an ontogenetic fashion. Humans and dogs do not visually signal with many of the same body parts. Humans do not possess tails that can be wagged, as a signal of agreeableness, or hackles that can be raised in warning. Humans also do not signal based on the position of their ears, another important form of communication in dogs. Likewise, dogs do not typically signal with their forepaws, and they do not have the ability to use a semantic language. Both domestic dogs and wolves do communicate with conspecifics through body movements, however—and while they may be able to respond to visual stimuli of individuals in another species with whom they have bonded, it is likely that individual experience of both dog and human play an important role in this.

Further support for an ontogenetic account of dog social behaviour comes from the fact that the very behaviours used to illustrate superior social skills in dogs (the following of a human point towards target objects) have been shown to improve with age and amount of experience even in human children. Udell et al. (2010) have called attention to the fact that research with human infants has found that infants begin to follow an adult's point after about nine months of age (Murphy & Messer, 1977), and they do not show the ability to follow a distal point (further than 50 cm) until 12 months of age (Lempers, 1979). The object-choice task used to study these skills in dogs (Hare, Brown, Williamson, & Tomasello, 2002; Miklósi et al., 2003) has also been conducted with human children (Behne et al., 2005; Lakatos et al., 2009), revealing in both cases that human children improved with age and experience across different variation of the pointing task. Given that individual development and experience appear to play a critical role in the development of these traits in

humans, it seems unlikely that ontogenetic experience would not be at least a partial requirement for communication between humans and dogs.

The Two Stage Hypothesis proposed by Udell et al. (2010) states that the sensitivity of a dog to human social cues depends on two types of ontogenetic experience. The first is interaction with humans during a sensitive developmental period, which ultimately leads to dogs accepting humans as social companions. This echoes Konrad Lorenz's discussion of what he described as a critical period in his pioneering work on imprinting in young animals (Lorenz, 1971). The second form of ontogenetic experience proposed by the Two Stage Hypothesis involves learning that is not restricted to a specific phase of development. This learning allows a dog to utilize the location and movement of parts of the human body to locate target objects, and includes both operant and classical conditioning.

Compelling evidence exists for both the Domestication Hypothesis (Hare & Tomasello, 2005; Miklósi et al., 2003) as well as the Two Stage Hypothesis (Udell et al. 2010). Proponents of the Two Stage Hypothesis often favour this explanation for its simplicity, as this alternative does not require the addition of a new mechanism, such as the evolution of human-like social cognition, during domestication. Furthermore, the idea of a developmentally sensitive period in which dogs acquire a special "preparedness" for interacting with other species can explain not just their relationship with humans, but also extend to their willingness to coexist with livestock and other animals that has been required of them in their various tasks. Those who champion the Domestication hypothesis continue to point to the obvious genetic basis of tameness in Belyaev's foxes, as well as a plethora of data demonstrating the "genius"-like ability of dogs (Hare & Woods, 2013) in interacting socially with humans. While the precise underpinnings of social cognitive ability in the dog

have yet to be determined, it should be noted these hypotheses are not mutually exclusive.   It seems that phylogeny and ontogeny, as is often the case, both play a pivotal role.

Physical Problem Solving

Many people who have owned or cared for either wild canids or wolf-dog hybrids report these animals to be very difficult to manage—they are known to be masterful escape artists, and very independent in nature relative to their domestic counterparts (Coppinger & Coppinger, 2001). A theoretical model proposed by Frank (1980) hypothesized that timber wolves *(Canis lupus occidentalis)* should perform better than dogs on problem-solving tasks requiring insight, such as the detour test created by Köhler (1927), which was later adapted by Scott and Fuller (1965) for use with 6-week-old domestic dog puppies. Frank and Frank (1982) subsequently developed a barrier task in order to test how dogs and wolves performed at finding a simple detour. Food was placed on the opposite side of a mesh fence that was either short (1m), long (7m) or U-shaped. Wolf puppies as well as Malamute dog puppies were tested for their ability to find their way around the fence in order to obtain food. Wolf pups significantly outperformed the dog pups, with the authors noting that while wolves appeared to use insight to solve the problem, dogs were reliant on repetition and trial-and-error learning.

Pongrácz et al. (2001) revisited the detour task, this time with an emphasis on human demonstration. In their version of the detour task, a favourite toy or food item was placed behind a V-shaped fence. Although dogs were able to solve this task, they did it more easily when they started from within the fence with the object placed outside it, rather than when their starting position was outside the fence, with the object inside the fence. Repeated detours starting from within the fence also did not help the dogs to obtain the object more

quickly if they subsequently experience a trial during which they started from outside the fence. Dogs were given six trials to attempt the detour from within the fence on their own, and did not improve significantly across these six trials. When dogs were first given the opportunity to watch a human demonstrator, however, their performance improved within 2-3 trials. Both owners and strangers were equally effective as demonstrators. Dogs did not copy the exact path of the demonstrator, suggesting that they were not simply mimicking the human, but rather were able to utilize the information provided by the demonstrator. A subsequent study (Pongrácz, Miklósi, & Csányi, 2005) also found that the dogs' ability to learn from a human demonstrator in a detour task is independent of the breed and age of the dogs. While there were no significant differences in latency among the different breeds, there was a trend for herding breeds to look back at the demonstrator more often than did sporting breeds. This difference may be a function of their work as sheepdogs, often needing to attend to a shepherd's directions. Overall, however, the results of this study suggest that the status of the domestic dog as a household pet likely has more influence on its performance in human-related tasks than its age or breed.

The detour task assesses spatial problem-solving abilities, requiring the subject to travel around a barrier to obtain a reward. In the absence of a human demonstrator, dogs generally perform poorly on this task and fail to improve performance significantly after repeated trials or to generalize problem-solving strategies when conditions are reversed. In contrast, wolves, have been shown to be more proficient at this task than their domestic counterparts (Frank & Frank 1982). Frank and Frank's version of the task, however, did not use the V-shaped fence used by Pongrácz et al. (2001). To determine how a wild canid might fare on the V-shaped barrier apparatus, Smith and Litchfield (2010) tested 20

sanctuary-raised dingoes (*Canis dingo)*, randomly allocated to one of four experimental conditions. These conditions included an inward detour (in which the dog started from outside the fence, and had to find its way to the reward inside of the V), and outward detour (in which the dog started from inside the fence, and had to find its way to the reward outside the fence), a doors open inward task (an inward detour task in which dogs could use an open door in the fence as a shortcut), and an inward detour task with a human demonstrator. Overall, dingoes completed the detour task successfully, with shorter latencies and fewer errors than dogs tested in previous studies. These results lend further support to the idea that captive-raised wild canids are more adept at nonsocial problem solving than are domestic dogs.

Dogs also seem to struggle with means-end connectivity. Frank and Frank (1985) gave both malamutes and wolves different variations of a task in which they had to attain a food dish by pulling a rope attached to the dish. While wolves immediately solved various versions of the problem, dogs were never able to solve the more complicated versions. In another version of a string pulling task (Osthaus, Lea, & Slater, 2005), dogs were required to pull on a string to remove a piece of food from a transparent box. The initial response of the dogs was to ignore the string and scratch at the unattainable food. Through trial-and-error, the dogs eventually learned to pull on the string, but only after dozens of trials. Dogs also did not appear to learn anything about the underlying cause of their success—if the position of the string was altered even slightly, the dog once again struggled to solve the problem. Importantly, when two crossed strings were used (with food attached to only one of the strings), dogs pulled on the string closest to the food (the incorrect choice), as they did not seem to understand that the string needed to be connected to the food. While little

understanding of means-end connection is demonstrated by dogs in the string pulling task, both primates (Beck, 1967; Jacobs & Osvath, 2015) and ravens (Osthaus, Lea & Slater, 2005) have been demonstrated considerable skill on variations of this task.

Riemer, Müller, Range, and Huber (2014) tested 34 Border collies in string pulling tasks in which the proximity of the reward to the connected string's end was varied. First, subjects were presented with a four-string task, in which four parallel perpendicular strings were used. One of these strings was baited, with the reward in line with the correct string's end. Dogs that performed above chance in this task were tested with a curved string task, involving one straight and one curved string. When the reward was attached to the curved string, it was equidistant from both strings' ends so that choosing by proximity was not possible. Only three of 20 dogs met criterion on this version of the string pulling task. The dogs also seemed to be unable to overcome their proximity bias in a parallel diagonal string task where proximity of the unconnected string's end to the reward was misleading. It was concluded in this study that although dogs may not demonstrate means–end understanding spontaneously, some can learn to pay attention to connectivity when proximity is not a confounding factor.

Range, Hentrup, and Virányi (2011) took another approach to the study of means-end connections in dogs, using an "on/off" task. In this task, the dogs had to choose between one of two moving boards—one board with a reward placed directly on top of it, or another board with a piece of food directly beside it. In order to make a selection, the dog was required to pull the board towards itself. The on/off task is a "support" problem, in which dogs must be able to understand connectivity between the board and the reward—they must choose the board with food on top of it in order to successfully obtain the reward. Thirty-two dogs were

tested under conditions in which: a.) both rewards were placed at an equal distance from the dog; b.) the on-board reward was more proximal to the dog; and c.) the off-board reward was more proximal to the dog. The dogs chose the correct board when both rewards were placed at the same distance from the dog, when the on-board reward was more proximal to the dog, and even when the off-board reward was food that was much closer to the dog. These findings suggest that the dogs clearly demonstrated an understanding of the connection between the board and the food. Interestingly, in the latter case, a variation of this task was also used in which instead of a direct reward, a token reinforcement was used. When dogs were required to retrieve a non-food object placed on the board in order to subsequently obtain a food reward, they did not perform above chance in this task. In contrast to previous string-pulling studies, this study showed that dogs are able to solve a means-end task, even if proximity of the unsupported reward is a confounding factor.

In a follow-up study, Müller, Riemer, Virányi, Huber, and Range (2014) tested 37 dogs with the same on–off task tested previously, and then tested subjects that passed this condition with three transfer tasks. For the *contact* condition, the inaccessible reward was touching the second board. For the *perceptual containment* condition, the inaccessible reward was surrounded on three sides by the second board, but not supported by it, whereas for the *gap* condition, discontinuous boards were used. Unlike in the previous study, the dogs did not perform above chance level in the initial trials of the on–off task, but 13 subjects learned to solve it. Their performance in the transfer tasks suggests that dogs can learn to solve the support problem based on perceptual cues, that they can quickly adopt new cues when old ones become unreliable, but also that some apparently inherent preferences are hard to overcome.

A dog's understanding of the physical world may be confounded by its predisposition to pay attention to human cueing. In one experiment (Bräuer, Kaminski, Riedel, Call, & Tomasello, 2006), dogs were given the choice between searching for food in one of two containers, each of which had been shaken by a human. In some cases, the container made a noise, and in other cases it did not. If dogs understand that objects make noise when they make contact with each other, then they should infer that the container making noise is more likely to contain food, and choose that container, rather than the one making no noise. Instead, dogs always chose the container which a human had touched—this suggests that the actions of the human were more salient to the dogs than the physical properties of the object. These finding are in contrast to those found with chimps, which in an analogous task would choose the container which made noise.

There is also some evidence that dogs are confused by the concept of gravity. Osthaus, Slater and Lea (2003) conducted four experiments with 56 adult dogs involving tasks in which food was dropped through an opaque tube connected either vertically or diagonally to one of two or three goal boxes. In the first experiment, modelled after studies with children and primates, the dogs first searched significantly more often in the location directly beneath the drop-off point (a gravity bias), although this box was not connected with the tube. The results were comparable to those of human infants and cotton-top tamarins in an analogous task (Hood, Hauser, Anderson, & Santos, 1999). Further experiments tested which problem solving strategy the dogs applied to find the food. Results indicated that they did not understand the physical mechanism of the tube itself, and would search in any one of the three available boxes. When the goal box (the correct location) was kept in the same location, the dogs learned to search there over trials, but when the location of the goal box

changed over trials, they showed no learning. These findings have been criticized, however, due to the fact that dogs may have followed the human's hand movements above the initial drop point as a cue in deciding where to search (Hare & Woods, 2013). More recently, researchers at the University of Toronto (Tecwyn & Buchsbaum, 2016) found that dogs consistently failed to demonstrate the gravity bias, and pointed out that much of the discussion of this phenomenon cited only one paper that had only *suggested* that this was a possible explanation for dogs' behaviour in the gravity task. This unfortunately led to numerous papers mistakenly citing the gravity bias in dogs as a known and thoroughly demonstrated phenomenon.

Overall, research in the area of physical problem solving in dogs has yielded two trends: (1) dogs tend to perform poorly on these tasks when they are non-social; and (2) domestic dogs are outperformed by wild canids (Frank & Frank, 1982; Smith & Litchfield 2010). Dogs are much better at these tasks, however, when a human demonstrator is involved (Pongrácz et al., 2001). Dogs perform poorly relative to other species on string pulling tasks (Osthaus, Lea, & Slater, 2005) but in some cases are able to learn to solve versions of this task, when proximity of reward is not a confounding factor (Müller, Riemer, Virányi, Huber, & Range, 2014). Dogs have also been successful in demonstrating behaviour consisting of means-end connectivity in a support task (Range, Hentrup, & Virányi, 2011) and have learned to solve more complex versions of this task (Müller, Riemer, Virányi, Huber, & Range, 2014). Conflicting findings such as those related to the gravity bias (cite), however, are a reminder of the need for carefully constructed experiments, and critical discussion of results.

Canine Attachment to Humans

It is well known that dogs excel at attending to human cues; this seemingly special relationship with humans has also raised other questions related to canine attachment to humans. One of the most important early methodological approaches with respect to the assessment of attachment in human infants has been the the Strange Situation Test (Ainsworth, 1969). This laboratory procedure was originally designed to examine the balance of attachment and exploratory behaviors under conditions of low and high stress in human infants. In this task, the infant is initially left alone in a room with its mother (experimenters observe from behind a two-way mirror). A stranger then enters the room, and the mother leaves. The mother then returns, and the stranger leaves. The mother then leaves, and the infant is left alone. Finally, the mother returns. Infant responses to this situation are customarily classified as fitting into one of three overall patterns of behavioral organization: *secure* (the infant shows signs of missing the parent upon separation, greets the parent actively upon reunion, and then settles and returns to play; *insecure-avoidant* (the infant shows little or no distress at separation from the parent and actively avoids and ignores the parent upon reunion; or *insecure-resistant* (the infant is highly distressed by separation and seeks contact on reunion but cannot be settled by the parent and may show strong resistance).

Topál, Miklósi, Csányi and Dóka (1998) tested 51 owner-dog pairs in a modified version of the Ainsworth (1969) task. The results demonstrated that adult dogs show patterns of attachment behavior toward the owner. Although there was considerable variability in dogs' attachment behavior to humans, the authors did not find any effect of sex, age, living conditions, or breed on most of the behavioral outcome variables. The human-dog relationship was described by means of a factor analysis in a 3-dimensional factor space:

anxiety, acceptance, and *attachment.* Classification of dogs could be categorized across these dimenstion in a way that was analogous to the secure-insecure attached dimensions of Ainsworth's (1969) original test. These findings suggest that a dog's relationship to humans is analogous to child-parent attachment behavior because the observed behavioral phenomena and the classification were similar to those described in mother-infant interactions.

In another study (Topál et al., 2005), dog and wolf puppies of the same age (16 weeks) were tested for their attachment towards their human caregiver. Selective responsiveness to the owner was found in the dog puppies, similar to that observed in adults. Extensive socialization, (by being hand reared) had only a minor effect on the attachment behaviour of dog puppies as they behaved similarly to normal pet dogs who had not been hand reared. Species differences however, were found between dog and wolf puppies. Although dogs were more responsive to their owner than to an unfamiliar human, wolf puppies did not behave differently towards familiar vs. non-familiar humans. These behavioural differences could be explained by assuming that selective processes took place in the course of domestication which are related to the attachment system of the dog.

True empathy is the ability to understand the feelings of another, to be able to "put yourself in their shoes". One suggested measure of empathy is contagious yawning—when someone yawns, or if one thinks or reads about yawning, they themselves are more likely to yawn in response. Some researchers have suggested that contagious yawning is related to our ability to respond to the emotions of others. Two key findings support this claim: the first is that contagious yawning in adult humans is positively correlated with high empathy scores (Platek et al., 2003). The other is that children with autism (a spectrum disorder in

which individuals often struggle to read the emotions of others) do not contagiously yawn (Senju et al., 2007). Research has found that 70% of dogs contagiously yawned in response to a yawning experimenter (Joly-Mascheroni, Senju, & Shepherd, 2007) and were much less likely to yawn if the experimenter simply opened his or her mouth but did not yawn. In another study (Silva, Bessa, & De Sousa, 2012), dogs listened to an audio recording of human yawning. Dogs were shown to contagiously yawn, but only when the recording was of a human that was known to them. Other research, however, using both a human demonstrator (O'Hara & Reeve, 2011) as well as video format (Harr, Gilbert, & Phillips, 2009), failed to replicate these findings. Furthermore, while the findings from human studies of empathy and autistic children are compelling and certainly worthy of further research, empathy is notoriously difficult to define, and not all researchers agree that contagious yawning is truly a measure of empathy (Yoon & Tennie, 2010). Another "wrench" in the study of contagious yawning is that yawning is also a common sign of stress or discomfort in dogs, meaning that any yawning behaviour exhibited in these studies should be interpreted with caution.

Constructs such as attachment and empathy are notoriously difficult to define and measure, even when dealing with human subjects, who can express themselves verbally. One solution to this problem is to find more discrete measures, such as hormones, which can be physically measured. Oxytocin is and ideal candidate, as it is a powerful neurotransmitter and is known to play an important role in pair bonding. When humans gaze into each other's eyes, or when a mother gazes at her newborn baby, oxytocin levels increase. Nagasawa et al. (2015) measured urinary oxytocin levels in dogs and their owners, and showed that such gaze-mediated bonding also exists between humans and dogs. Urine tests before and after

the session revealed that oxytocin levels spiked in people whose dogs stared at them the most, and their dogs experienced a similar effect, with a rise in their own oxytocin levels. Wolves, who rarely engage in eye contact with their human handlers, did not show the same effect. Human-like modes of communication, including mutual gaze, may have been acquired by dogs during domestication with humans. These findings support the existence of an interspecies oxytocin-mediated social attachment via gazing. This process could have supported the co-evolution of human-dog bonding by engaging common modes of communicating between dogs and humans.

Anthropomorphism, and Human Perception of Dog Cognition

Though it is hard to generate an exact figure, in the United States, Canada, and Eastern Europe, there are estimated to be 73 million, 6 million and 43 million pet dogs, respectively (Psychology Today, 2012). Even the most casual dog owner speculates about the cognitive world of his or her pet—this has resulted in an amount of public interest that is not typical of most areas of comparative cognition. This widespread interest in the topic of dog cognition has resulted in the appearance of many new labs, some dedicated exclusively to the study of dog cognition. Human interest in canine social skills have a longstanding history—in an early anecdote, Romanes (1882) reported the case of a hunter who fell through the ice on a frozen river. His dog "made many fruitless efforts to save his master, and then ran to a neighboring village, where he saw a man, and with the most significant gestures pulled him by the coat and prevailed on him to follow. The man arrived on the spot in time to save the gentleman's life" (p. 447). It is not uncommon to hear even today anecdotes of canine heroes—dogs who have alerted their owners of impending danger or who have sought help for an owner in distress. Are these instances of coincidence or expanded accounts of

dog behavior with a simpler explanation? Or, do dogs actually understand the nature of an emergency and take appropriate action?

Macpherson and Roberts (2006) carried out two studies which questioned the behavioural response of dogs in a perceived emergency scenario. Importantly, this study borrowed the bystander apathy paradigm (Darley & Latané, 1968) from human social psychology research. Bystander apathy experiments show that when a person is in danger, they are more likely to receive help when there are few bystanders available to help than when there are many. This is explained as a diffusion of responsibility—the more bystanders that are available, the less responsibility any one individual feels to act.   Macpherson and Roberts (2006) used conditions in which one or two bystanders were available; the bystander(s) did not respond to the emergency, and the question was whether the dog would go to a bystander for help.

In the first dog emergency scenario, an owner walked into a field with her dog, as if on a normal walk. Once she reached the center of the field (indicated by a target painted on the ground), the owner clutched her chest, and feigned symptoms of a heart attack. The owner then collapsed to the ground, and remained motionless for 6 minutes. One or two bystanders seated nearby could be gone to for help. At the other end of the field, a cameraman was hidden behind a tree, recording the dog's behavior. Experimenters measured how long dogs engaged in certain behaviours (e.g.: time spent in proximity to owner, time spent in proximity to bystander) as well as the frequency of certain behaviors (e.g.: how often they touched the owner or bystander, how often they barked). Contrary to popular belief, no evidence was found that the dogs were attempting to seek help for their owner. Rather, they

spent most of their time in proximity to the owner, rather than the bystander. There were no significant differences between dogs in the one bystander versus two bystander conditions.

If a dog truly has insight into an emergency scenario, the dog might assume that it did not need to alert the bystanders, as they could plainly see the endangered owner for themselves. Alternately, it is possible that the dog simply thought the owner was sleeping, or playing a game with it. In light of these limitations, a second experiment (Macpherson & Roberts 2006, Experiment 2) was designed, in which a more explicit emergency was created. This experiment took place indoors, and in two separate rooms. When the dogs entered the building with their owner, they went into the first room, where the owner met and shook hands with a bystander. The dogs then proceeded to the second room, now aware of the availability of the bystander, who could not see any of the activity in the main room. Once in the main room, dogs in the experimental group watched as a bookcase toppled onto their owner, leaving her trapped beneath. For 6 minutes, the owner explicitly appealed to the dog for help. In a control group, the owner simply stood next to the bookcase for 6 minutes looking at books, and no emergency occurred. In both conditions, the dog's behaviors were filmed by an overhead camera.

Even with an owner explicitly appealing for help, in no case did dogs seek the help of the bystander in the adjoining room. One pronounced difference was that control dogs spent much more time roaming or exploring their surroundings, whereas dogs in the experimental group, like those in Experiment 1, tended to remain in close proximity to their owner. Dogs are a social animal, and so it seems reasonable that they would prefer to stay by the side of their master. However, both of these experiments suggested that dogs had no insight into the nature of the emergency and thus did not seek help for their owners. This is not to say that

dogs are not capable of "heroic" acts—this is seen every day with police dogs and various types of service dogs. These heroic behaviors, however, appear to be the product of training rather than understanding an emergency situation, and thus do not support the domestication hypothesis.

Anthropomorphism is regularly used by owners in describing their dogs. It is of interest to determine whether any of these attributions of dog understanding are legitimate, or whether humans are simply projecting human psychological phenomena to non-humans. Anthropomorphism has long been treated with caution in animal cognition—in response to Romanes' "anecdotal" accounts of animal behaviour, C. Lloyd Morgan (1901) proposed what is now a fundamental precept of animal cognition research and states "In no case is an animal activity to be interpreted in terms of higher psychological processes if it can be fairly interpreted in terms of processes which stand lower in the scale of psychological evolution and development" (p.59). Morgan used his own dog, a terrier named Tony, as an example in applying his cannon. Tony had learned to unlock a gate and let himself out of the yard for unsupervised strolls. Even today, a casual observer might infer that Tony had a working knowledge of the gate locking mechanism—Morgan, however, was able to demonstrate that Tony had no real understanding of how to unlock the gate. Rather, he had acquired the appropriate behavioural response through trial-and-error, eventually arriving at a successful combination of movements to unlock the gate.

In another historical incident dating back to the early 1900's, a horse named "Clever Hans" toured the world for what were thought to be exceptional human-like abilities. Most famously, Hans was believed to be able to count. Hans' owner, William Von Osten would ask Hans a mathematical problem, and Hans would stomp his hoof the correct number of

times to indicate his response. Eventually, it was revealed that Hans was not actually counting; rather, he was picking up on very subtle head movements from Von Osten, indicating when he had arrived at the correct number and should stop stomping his hoof. Importantly, this was not fraud on Von Osten's part—he legitimately believed in Hans' abilities and had no idea that he had been cueing him. He is said to have been very upset when he learned the truth, having felt "deceived" by the horse. Clever Hans has since become a cautionary tale in animal cognition research, a reminder that when designing studies, caution must be taken to assure that there are no subtle cues provided to the animal by a human experimenter. Given their strong inclination to pay attention to human caregivers, Clever Hans cues are particularly important to avoid in studies of the domestic dog.

One attribution commonly made to dogs is that they can display a "guilty look" when they have disobeyed their owner, or have otherwise been caught in a forbidden act. Morris, Doe, and Godsell (2008) found in a survey of 307 dog owners that the majority believed that their dogs felt emotions such as sadness, joy, surprise, and fear. Seventy-four percent also said that their dog experienced guilt. A "guilty look" is clearly recognized by owners and non-owners alike, and involves such things as avoidance of eye contact, submissive posture, and tucked ears and/or tails. Among human observers, it is a small step from identification of a dog's guilty look to the assumption that the dog in fact understands what it has done and feels guilty. Konrad Lorenz (1954) also spoke liberally of guilt in dogs, saying that we can "assume with certainty that (the dog) hides a guilty conscience" (p.183). Lorenz also theorized that different breeds of domestic dog were descended from different wild canid ancestors. For example, sighthounds such as the greyhound or Ibizan hound might descend

from jackals (*Canis aureus*; many sighthounds share some physical traits with the jackal, and many were developed in regions of the world inhabited by jackals), while spitz-type breeds such as the Siberian husky or Alaskan Malamute might descend from wolves (which likewise share similar physical features and geographic location). Advances in genetic research have since allowed us to determine conclusively that all domestic dogs are descended from the Gray wolf, and are in fact now considered a subspecies of the Gray wolf; in fairness to Lorenz, however, who did not have access to this technology, he is also known to have stated later in life that "…everything (he'd) written about dogs was wrong" (Coppinger & Coppinger, 2001, p.35).

One early study (Vollmer, 1977) found that one dog (a husky) in a single study behaved in a "guilty" fashion regardless of whether it was he or his owner who had made a mess of the living room. In a more thorough exploration of the guilty look, Horowitz (2009) observed the behaviour of 14 dogs, which were videotaped and analyzed for behaviours that corresponded to owner descriptions of a guilty look in dogs. Dogs were first forbidden by their owners to take an item of food, at which point the owner left the testing area. The food item was then either consumed by the dogs or removed by the experimenter. Results revealed that dogs were just as likely to display a guilty look, regardless of whether or not they had consumed the food. Furthermore, the guilty look was seen more in trials in which the owner had scolded their dog—these effects were more pronounced when the dog had been obedient, rather than disobedient. Results of this study suggest that the dogs' behaviour were not the result of guilt, but were rather a fear-response to being scolded by their owner.

Despite evidence to the contrary, it is not hard to find a dog owner who will quickly insist not only that his or her dog exhibits the guilty look, but does so in the absence of any

prompting. For example, people insist they know the second they walk in the door that their dog has chewed something it should not have, based on the dog's face and behaviour (Hecht, Miklósi, & Gácsi, 2012). To explore this further, Ostojić, Tkalčić, and Clayton, (2015) investigated whether a dog's' own actions or the evidence of a misdeed might serve as triggering cues. The experimenters manipulated whether or not dogs ate a forbidden food item, and whether or not the food was visible upon the owners' return. Based on their dogs' greeting behaviour, owners were not able to determine beyond chance expectancy whether their dogs had or had not eaten the forbidden food. Dogs' greeting behaviours were also not affected by their own action or the presence (or absence) of food. These findings support the work of Horowitz (2009) and suggest that dogs do not demonstrate the guilty look in the absence of a cue indicating that they will be reprimanded by their owner.

Taken together, the above studies suggest that typical owner assumptions of canine understanding and awareness are often more sophisticated than the behaviours observed in empirical studies would suggest. Given our close relationship with the domestic dog, humans are more likely to anthropomorphize certain aspects of their personality and behaviour (Morris et al., 2008). Likewise, dogs are more likely to pick up on subtle human cueing than most species—resulting in a need to ensure strict research methodology and interpretation of results.

Studies of "Higher Order" Cognition in Dogs

In a series of experiments designed to study dogs' understanding of human intentions, Petter, Musolino, Roberts, and Cole (2009) asked if dogs could detect human deception. Dogs were allowed to choose between two opaque containers, one containing food and the other empty. The containers were separated by 3 m, and the left-right position of the baited

container changed randomly among trials. Two people, previously unknown to the dog, alternately stood behind one container and verbally encouraged the dog to approach that container. One person served as the "cooperator." This person always stood behind the baited container, and thus approaching this person always led to food reward. The other person served as a "deceiver." This person always stood behind the empty container. When the dog approached and examined the empty container, the deceiver went to the other container, took the food in it and pretended to eat it. Of interest was how dogs would respond to deception over a number of trials given over five sessions. It was found that dogs continuously approached the container in front of the cooperator. On deceiver trials, however, dogs began to avoid the deceiver. On trials when they did so, they often went to the alternate container containing food reward.

One explanation of these findings is that dogs have Theory of Mind. That is, they impute positive and negative intentions to humans cueing them. In a final experiment, Petter et al. (2009) used inanimate cues (black and white boxes) as the "cooperator" and "deceiver". The results were the same as those using humans to cue the dogs; the dogs learned to approach the "cooperator" box more often than the "deceiver" box. The findings indicated that dogs were sensitive to the correlation between cues and their outcomes, but offered no support for the idea that dogs understand human intentionality.

Theory of mind has also been addressed by Udell, Dorey and Wynne (2011) through the use of a perspective taking task. In this experiment, wolves, shelter dogs, and pet dogs were all given the choice of begging from a person who faced them (the seer) over a person whose back was turned to them (a blind experimenter). The question asked in this task is whether dogs understand that a person who sees them will know that they are begging for

food but that a person who does not see them will not. Overall, pet dogs chose the seer more often than did shelter dogs and wolves. All types of subjects tested showed significant preference for the seer when the blind individual's back was turned to them, but only pet dogs tested indoors and outdoors showed a significant preference when a book covered the blind individual's eyes. None of the canine groups showed a significant preference for the seer when a camera covered the blind individual's eyes, and only pet dogs tested indoors significantly preferred the seer when a bucket covered the blind individual's eyes. In a second study, dogs and wolves more readily begged food from a seer with a bucket on her shoulder than from a blind individual with a bucket on her head.

Udell et al. (2011) argued that their findings can best be explained through associative learning (that is, the preexperimental learning of subjects to attend to humans) and that these findings challenge predictions from both the domestication hypothesis and theory of mind accounts of dog behaviour. The fact that wolves significantly preferred the seer when the blind individual had her back turned seems to challenge the domestication theory that wolves do not attend to human cues in an inherent fashion the way that dogs do. Likewise, the failure of some groups of canines to prefer the seer when the blind individual's eyes were covered seems to challenge the theory of mind prediction that dogs should recognize the blind individual as one who cannot know that they are begging. From an associative learning position, however, decline in preference for the seer in the book, camera, and bucket conditions, relative to the back-turned condition, can be explained by differential stimulus generalization. That is, an experimenter facing the dog, even with an occluder over his or her eyes, looks more like the seer than does an experimenter whose back is turned. Pet dogs may

do better on these tasks (book and bucket) because they have been overtrained to approach a person with eyes visible through pre experimental occasions of begging and feeding.

Roberts and Macpherson (2011) agreed with Udell et al. (2011) that these findings are best interpreted within a learning context. However, they also suggested that these experiments are not optimal tests of either domestication or theory of mind, because they "stack the deck" against these alternative theories. Given that the wolves used in this experiment were raised by humans and had participated in other behavioral experiments, they must have been fed on a number of occasions by a human facing them. Even if a wolf has no interest in human social cues, it would still surely learn that it was fed by this neutral object. The perspective-taking task, then, may not be a good test of the domestication theory or of theory of mind in dogs, as the use of this task, combined with preexperimental learning in all the subjects, strongly biases the outcome in favor of a behavioral learning interpretation. Tasks less influenced by preexperimental training would provide less confounded tests of domestication and theory of mind.

One condition used by Povinelli and Eddy (1996) with chimpanzees might have proven informative regarding the question of theory of mind in dogs. In this condition, both experimenters had their backs turned to the chimp, but one person looked over her shoulder at the subject. Thus, both experimenters appeared in a nonconventional position for begging (backs turned), but the chimp could see the eyes of one experimenter. Chimps tested surprisingly showed no preference for the person whose eyes they could see. This finding was pivotal in leading Povinelli (2000) away from a theory of mind interpretation of chimpanzee understanding of human visual gaze. It suggested that simply seeing a human from the front was a cue for begging and that seeing eyes played no special role. Such an

experiment with dogs might provide crucial evidence for or against theory of mind in canines.

Closely related to theory of mind in human cognition is *metacognition*, or awareness of the contents of one's own memory. To address the question of whether or not dogs demonstrated any abilities consistent with metacognition, McMahon, Macpherson and Roberts (2010) conducted an information seeking study. In the initial experiment, dogs were trained to choose among four different boxes, each with a food tray and potential food reward underneath. The boxes were all black, with the exception of one box that had a white side. The box with the white side always had a food reward underneath it, while the black boxes did not. Initially, the dogs were trained with the boxes facing them front-on, such that the white-sided box was fully visible. The dogs quickly learned to choose the box with the white side. The boxes were then rotated 45 degrees (such that the white side was still easily visible) and 90 degrees (such that the white side was still partially visible). The dogs' percentage of correct choices progressively declined across these conditions. Finally, the boxes were rotated to 135 degrees, making it impossible for the dogs to see the white side from their starting position. If the dogs were aware that they could seek information, then given their extensive training they should have realized that they could walk around to the back of the boxes to determine which box had the white side. The dogs failed to do this and did not choose the correct box above chance. Even when the dogs were given guidance training, in which they were walked behind the boxes to show them that it was simply the orientation that had changed, the dogs still failed to seek information about the white side on test trials.

Dogs have been selectively bred and trained to pay attention almost exclusively to humans. In a follow-up study, McMahon et al. (2010) attempted to determine whether dogs might seek information in a human-oriented context. In this task, dogs had to choose one of three identical boxes to knock over, only one of which had a food reward hidden beneath it. Prior to selecting a box, the dog first had to choose between two humans—one was an informant, who would point to the location of food, and the other was a non-informant, who would turn her back to the dog, providing no information. Both humans were females of similar height and dress, and both had no previous association with the dog. Dogs rapidly developed a statistically significant preference for the informant. Thus, this study suggests that dogs may seek needed information when they are unaware of the location of a food reward, but they do so only when the source of that information is a human informant.

Language and Syntax in Domestic Dogs

Elements of language acquisition have also been studied in the domestic dog, with the two most notable cases being those of Rico and Chaser. Rico, a border collie, knew the labels of over 200 different items (Kaminski, Call, & Fisher, 2000; Bloom, 2004). Rico inferred the names of novel items by exclusion learning and correctly retrieved those items right away as well as 4 weeks after the initial exposure. This was considered evidence of "fast mapping", a process through which a subject develops a quick and rough hypothesis about the meaning of a word--and historically used to describe word acquisition in human children (Heibeck & Markman, 1987; Markson & Bloom, 1997). Subsequently, another border collie named Chaser was shown to have learned the names of 1022 objects over the course of three years of intensive training (Pilley & Reid, 2010). Interestingly, Chaser also demonstrated an ability to learn words by inferential reasoning by exclusion—that is, she

inferred the name of a novel object based on its presence among other objects for which she already knew the names. Chaser has also demonstrated some basic understanding of syntax (Pilley, 2013). When taught sentences consisting of a prepositional object, a verb, and a direct object, Chaser successfully learned to act on commands based on their grammatical structure. For example, Chaser would correctly perform the command "to ball take frisbee", and would perform the opposite behavior if given the command "to frisbee take ball". These finding are similar to those found in early studies of dolphin syntax (Herman, Kuczaj, & Holder, 1993; Herman, Richards, & Wolz, 1984), and suggest sophisticated communicative ability in the domestic dog.

Conclusion and Present Studies

The preceding discussion of dog cognition studies may come across as a curiously exhaustive summary—this was intentional, and meant to underscore the fact that, to date, the vast majority of studies in dog cognition have been focused on elements of social cognition, with both phylogenetic and ontogenetic explanations proposed by numerous researchers. While debate still exists as to exactly how dogs arrived at their unique cognitive skillset, it is generally agreed that two trends exist in the data gathered across an increasing number of studies. The first is that dogs appear to be "genius-like" (Hare & Woods, 2013) when it comes to any type of task that involves following human cues. Examples of such tasks include object-choice tasks with the use of human pointing gestures or cues (Hare & Tomasello, 2002; Miklósi et al., 1998), detour tasks (Pongrácz et al., 2001), and tasks involving choice between an informative vs. non-informative human (McMahon et al., 2010; Petter et al., 2009). The second trend is that dogs often appear to be clueless when left to their own devices to act on a task. This includes their failure to seek help for a human who

appears to be in distress (Macpherson & Roberts, 2006), as well as their difficulty in information seeking tasks which are not human-directed (McMahon et al., 2010). Dogs also appear to fail to understand means-end connections without extensive training, such as the string-pulling task (Osthaus et al., 2005). The question of cognitive processes in dogs is therefore complicated and rife with questions for future research.

The interest in social cognition with respect to the domestic dog is intuitive, given our close relationship with these animals. There remain, however, comparatively few studies examining fundamental aspects of cognition in dogs. The processing of number, time, and space, for example, are crucial elements of cognition, which help an animal to survive in its day-to-day life. An animal will benefit from knowing roughly how many food items or how many predators are in front of it; likewise, it will benefit from knowing how long it has been since it found food, as well as the location of its home. Although these are processes which have been studied for decades in rats, pigeons, monkeys, and other more "typical" lab species, very little on these topics has been published with respect to the domestic dog. To have a full understanding of canine cognition, an understanding of these basic cognitive processes is required. Given that dogs have been selectively bred to attend to humans, it is entirely possible that we have "bred out" cognitive traits that would have been necessary for their wolf ancestors. The following chapters will therefore address issues related to a.) numerical discrimination, b.) interval timing, and c.) spatial memory, respectively. These projects have benefitted from the fact that these topics are well studied in other species, and thus previous literature in all three areas has been drawn upon in order to develop apparatus and procedures for testing these abilities in the domestic dog.

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Chapter 2

Can Dogs Count?

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Abstract

Numerical competencies have been thoroughly examined in several species, yet relatively few studies have examined such processes in the domestic dog. In an initial experiment, procedures from numerical studies of chimpanzees were adapted for use with 27 domestic dogs. Subjects in these experiments watched as a different numbers of food items were sequentially dropped into each of two bowls. The subjects were then allowed to select and consume the contents of one of the bowls. Although dogs excelled in a 1 vs 0 condition, their performance failed to significantly surpass chance across all other ratios. In a second experiment with a single subject (a rough collie named Sedona), the procedure was revised so that non-food stimuli were presented simultaneously to the dog on two magnet boards. If Sedona chose the board with the majority of the items, she was rewarded with a piece of food hidden underneath the board. If she made an incorrect choice, she received no reinforcement. Interestingly, Sedona's performance far exceeded those of the dogs in Experiment 1. Implications of these findings for the study of domestic dogs are discussed.

Keywords: dogs, canine cognition, counting, numerical discrimination, Weber's Law

Can Dogs Count?

As humans we use number in almost every facet of our lives—we count how much money we have, check the temperature before we go outside, and look at our watches for the time. Numerosity is also an important function for non-human animals in their day to day existence—knowing how much food is available, how many offspring one has, or how many predators are approaching may all very well be useful survival skills. Precise counting and arithmetic as we know them are the result of language and culture—thus, these are uniquely human skills. There exists among humans, pre-verbal human infants, and non-human animals, however, an evolutionarily more primitive system of numerical discrimination, the approximate number system (ANS; Merritt, DeWind, & Brannon, 2012). According to the ANS, number is represented internally on a continuous, linear number line, which allows both humans and non-human animals alike to discriminate approximate magnitudes. Even human tribes with no formal system or language to represent number (e.g., the Pirahã and the Mundurukú) are able to discriminate numerosity using the ANS (Gordon, 2004; Pica, Lemer, Izard, & Dehaene, 2004). Number only becomes a discrete representation in human language when number symbols become mapped onto these approximate magnitudes through learning during childhood. It is from this shared and primitive system that number symbols and the more precise use of number that is typical of adult humans has presumably risen.

Cardinality, Ordinality and the Internal Representation of Number

Number takes three forms—cardinal, ordinal, and nominal numbers. Cardinality refers to the elements of a set, and essentially asks the question "how many". Ordinality refers to the rank of an item (e.g., fourth place). Nominality concerns assigned numbers (e.g., the number an athlete wears on his jersey) and is therefore a uniquely human practice.

Studies of numerosity in non-human animals are thus concerned exclusively with cardinal and ordinal number. One major issue with regard to number is whether it is represented by the ANS and/or by an object file system (Brannon, 2004; Carey, 1998; Feigenson, Dehaene, & Spelke, 2004). The ANS maintains that numbers are represented internally and continuously as an approximate magnitude on a number line. There is no upper limit to the approximate number system, but it does become systematically less precise as number increases.

One of the hallmarks of the ANS is that it obeys Weber's law. Weber's law states that the change in stimulus intensity needed for an organism to detect a change is a constant proportion of the original stimulus intensity, rather than a constant amount. Two effects that are seen as a result of this are the *distance* effect and the *magnitude* effect. The distance effect maintains that the greater the distance between two numbers, the easier they will be to discriminate (9 vs 1 will be easier to discriminate than 3 vs 1). The magnitude effect is the common finding that when distance is held constant, larger numbers are harder to discriminate than smaller numbers (2 vs 1 is easier to discriminate than 9 vs 8).

Ratio effects in accordance with Weber's law have clearly been demonstrated with pigeons. Using an operant conditioning chamber, Roberts (2010) showed pigeons three different combinations of red and green light flashes, using ratios of 2 vs 1, 3 vs 2, and 4 vs 2. The use of these particular ratios was important because the distance between numbers is 1 for 2 vs 1 and 3 vs 2, but increases to 2 for 4 vs 2. The ratio between numbers, on the other hand, was equal for 2 vs 1 and 4 vs 2, but smaller for 3 vs 2. If distance was controlling the performance of the pigeons, then it should be have been found that 4 vs 2 was most easily discriminated, while 2 vs 1 and 3 vs 2 were harder but equally discriminable. Instead, it was

found that 2 vs 1 and 4 vs 2 were equally discriminable, while 3 vs 2 was significantly more difficult to discriminate. This finding suggests that ratio, not distance, was controlling the performance of the birds.

While the analogue magnitude system is generally an accepted account of numerical representation, another system known as the object file system is more controversial. The object file system (sometimes referred to as "subitizing") deals only with small numbers, specifically numbers 1-4. These numbers are thought to be mapped discretely in a one-to-one represention, making them instantly accessible. For example, if subjects are shown four dots on a screen, they do not need to systematically count the dots because they will immediately recognize that there are four dots.

In support of the object file system, Hauser, Carey, and Hauser (2000) found that wild, untrained monkeys were able to discriminate and successfully choose a larger number of food items over a smaller number of food items. Over 200 semi-free-ranging rhesus monkeys watched as experimenters placed pieces of apple into each of two containers. The experimenter then walked away so that the monkeys could approach the containers. When the containers contained 1 vs 2, 2 vs 3, 3 vs 4 or 3 vs 5 slices of apple, the monkeys chose the container with the greater quantity of food. Interestingly, however, when the number of items to be counted exceeded the number four (4 vs 5, 4 vs 6, 4 vs 8, or 3 vs 8) the monkeys were unable to reliably choose the container with the most food. Hauser et al. suggested that the breakdown in performance of the monkeys when the number exceeded four items is evidence that the monkeys were using a spontaneous number system (i.e., the object file system) as opposed to an analogue magnitude system in order to solve the problem.

In subsequent laboratory studies, Beran and colleagues (Beran, 2001; Beran & Beran, 2004) conducted experiments analogous to those of Hauser et al. (2000), in which chimps watched as an experimenter sequentially dropped pieces of food (M&Ms or pieces of fruit), one-by-one, into each of two bowls. The chimp was then allowed to choose one of the two bowls and consume its contents. In this laboratory task, chimps discriminated magnitude well beyond 4 items, and up to 10 items. The most persuasive argument against the use of an object file system is that even with numbers 1-4, both humans and non-human animals demonstrate the ratio-effects that are the signature of the ANS (Beran & Rumbaugh, 2001). If the one-to-one representation suggested by the object file system were in fact being used, then these ratio effects should not be seen for the numbers 1-4.

A major criticism of laboratory studies with non-human animals is that with extensive training and a large number of trials, the subjects may simply be learning the correct response to a problem associatively, rather than engaging in higher level cognitive processing. Brannon and Terrace (1998) controlled this issue in a study of numerical discrimination by monkeys. In this ordinal task, two monkeys were first trained to order arrays of 1-4 items in ascending order. Unlike the Beran (2001; Beran & Beran 2004) studies, which used sequential presentation, these items were presented simultaneously, on a computer screen. Importantly, as a control for non-numerical cues, the items were varied in size, shape, and color. The monkeys were later tested, without reward, on novel pairs of stimuli from arrays of 5-9 items. Both monkeys were able to spontaneously order the new values, which suggests not only that their numerical ability was not the result of extensive laboratory training, but also that an analogue magnitude system was being employed by the monkeys. Similar findings have also recently been found with pigeons (Scarf, Hayne, & Columbo,

2012). In another study, Cantlon and Brannon (2006) trained monkeys to order pairs of numerical stimuli with the values of 1-9. Once the monkeys learned to order these values, they were introduced to pairs of novel displays of 10, 15, 20 and 30 items. Once again, monkeys were able to spontaneously order the novel values, suggesting that there is no known upper limit on the numerical capacity of these animals.

Evidence from Neuroscience

Evidence from single cell recordings has implicated the intraparietal sulcus (IPS) as the primary brain structure involved in numerical processing. Although it was originally thought that the IPS might contain a specified number module, evidence now suggests that the IPS serves a "patchwork" of different functions (Ansari, 2008). The prefrontal cortex (PFC) is also involved in numerical processing. Response latencies are faster in the IPS than in the PFC, however, suggesting that the IPS extracts numerical information and subsequently sends the information to the PFC for processing (Nieder & Dehaene, 2009).

In a delayed matching to sample task (Nieder & Miller, 2004), monkeys were shown an array of 1-5 items and subsequently had to decide if a sample array matched this number. Single-cell recordings, remarkably, showed that the monkeys had numerosity selective neurons, which fired preferentially to a "preferred" numerosity. Neurons thus appear to be "tuned" for specific numerosities. These tuning curves are imprecise, such that a neuron with a "preference" for 4 will also fire for 3 and 5. The resulting tuning curves do a good job of explaining the distance and magnitude effects associated with the analogue magnitude system. When two numbers are farther apart, their respective tuning curves will overlap less, creating less "noise" around the number and making them easier to discriminate. Tuning curves, however, get wider and less precise as numerical magnitude increases. Thus, while 1

vs 2 will have narrower tuning curves that are more precise, 8 vs 9 will have broader tuning

curves that overlap more with surrounding numbers, making discrimination more difficult.

Numerosity in the Domestic Dog

Although psychological studies of the domestic dog have increased dramatically over

the past decade (Miklósi, Topál, & Csányi, 2004), very few studies have addressed numerical

cognition in the domestic dog. In one study (West & Young, 2002), a version of the

preferential looking technique that had previously been used with infants (Wynn, 1992) and

monkeys (Flombaum, Junge, & Hauser, 2005) was adapted for use with dogs (Also see

Pattison, Laude, & Zentall, 2013, in this volume). In this task, dogs watched as food items

were placed, one at a time, behind a screen and out of their view. The screen was then lifted

so that the dog could see the resulting number of items. In one condition, dogs saw a simple,

correct calculation ($1 + 1 = 2$). In two other conditions, however, dogs either saw an

unexpected outcome in which fewer objects were present when the screen was lifted than

should be expected ($1 + 1 = 1$), or saw an outcome in which more objects resulted than

should be expected ($1 + 1 = 3$).   When an expected outcome was used, dogs spent as much

time looking at the outcome as they did looking at the initial presentation of items, but, when

a result was unexpected, dogs spent significantly longer looking at the resulting amount of

food. This suggests that, like infants and monkeys, dogs may have been anticipating the

outcome of the calculations, which would require them to employ some form of numerical

system.

Ward and Smuts (2007) also sought to study numerical ability in dogs, by examining

the ability of dogs to choose a larger over a smaller quantity of food. Pieces of hotdog were

presented simultaneously to dogs on two plates. Ratios used in the initial experiment

included 1 vs 4, 1 vs 3, 2 vs 5, 1 vs 2, 2 vs 4, 3 vs 5, 2 vs 3, and 3 vs 4. Of the 29 dogs originally tested, 15 dogs (three dogs did not complete the task and eight dogs were eliminated due to laterality bias) chose the plate containing the larger quantity of food, and the performance of these dogs across ratios between numbers of food items conformed to Weber's law. In a second experiment, two dogs from Experiment 1 were presented with food on two plates, but this time the plates were covered so that the dogs would have to make their choice without being able to see the food. In one condition, the plates were presented and covered simultaneously, while in a second condition, the plates were presented and covered successively. In all cases, however, the dogs were at some point allowed to view the complete amount of food on the plate. While the dogs' selection of the greater quantity of food was significantly above chance, findings for magnitude and distance effects in accordance with Weber's law were mixed.

The present experiment sought to further investigate numerical ability in the domestic dog. Although numerical ability has been well established in other non-human animals, aside from the West and Young (2002) and Ward and Smuts (2007) studies, almost none of this research has to date focused on dogs. Experiment 1 adapted the paradigms used by Beran (2001; Beran & Beran, 2004) and Hauser et al. (2000) with chimpanzees and monkeys , such that dogs watched as items were sequentially dropped into each of two bowls for a potential food reward. Experiment 2, on the other hand, incorporated simultaneous presentation of items, consistent with Brannon and Terrace's (1998) work with monkeys. Although both chimps and monkeys have been successful in numerical tasks with sequential presentation of items, there is evidence that monkeys more easily discriminate numerosity in

tasks that use simultaneous presentation (Nieder, Diester, & Tudusciuc, 2006). It is therefore worthwhile to explore the effects of both methods of presentation in the domestic dog.

Although Ward and Smuts (2007) also used a two-choice task, their dogs were limited to smaller numbers of items, and performance did not consistently conform to Weber's law in their second experiment. Additionally, the Ward and Smuts study allowed the dogs to view the contents of the two plates of food stimuli. This is a potential confound, as it could be argued that the dogs were making a volume-based rather than a numerically-based judgement. The present study controlled for this possibility by not allowing the dog to see the food once it had been placed in a bowl (Experiment 1) or only rewarding the dog after it made the correct choice (Experiment 2). Several issues were explored, including the use of sequential versus simultaneous presentation of items, the use of a broad number of items (both below and above the number four), the use of novel ratios, and, uniquely, the use of a human-directed versus a non-human-directed task.

Experiment 1

In Experiment 1, we examined numerical cognition in domestic dogs, using a procedure similar to those used in the Beran (2001; Beran & Beran, 2004) and Hauser et al. (2001) studies of chimpanzees and monkeys. In these studies, food pieces were sequentially dropped into each of two bowls. The subject was then allowed to choose one of the bowls and to consume its contents. This procedure was chosen in order to find out if dogs could discriminate between different numbers of sequential events. If dogs can discriminate the numerosity of a series of salient events, they should choose the bowl with the greater quantity of food. Several variations on this task were attempted and are outlined below. As with other

studies of numerical cognition, accuracy of the subject's selection across different food ratios should obey Weber's law and thus demonstrate magnitude and distance effects.

Method

Subjects.

The subjects were 27 dogs of multiple breeds (seven dogs in Experiment 1a, seven dogs in Experiment 1b, nine dogs in Experiment 1c, and four dogs in Experiment 1d). All dogs were between the ages of 1-10 years old. Dogs were recruited through the assistance of local dog obedience schools or through associates of the experimenters.

Materials.

Two identical bowls were used for this experiment. The bowls were perforated, and had false bottoms containing extra food, in order to control for any olfactory cues that might guide the dog to the bowl containing the most food. Each bowl was 20 cm in diameter and was bolted to a piece of plywood measuring 50 cm x 50 cm. The plywood acted as an anchor for the bowl, and discouraged the dog from moving or picking up the bowl.

Procedure.

Experiment 1a. This task most closely replicates the Beran (2001; Beran & Beran, 2004) numerical tasks with chimpanzees, and all subsequent variations presented were modifications of this task. The two bowls were placed 3.65 m apart, from the inside edge of each bowl. The experimenter stood 1.83 m away from the midpoint between these two bowls. The dog, with its handler, also stood 1.83 m away from the midpoint between the bowls, but on the opposite side from the experimenter (See Figure 2.1). The dog watched as the experimenter approached the first bowl, and dropped pieces of food, sequentially, into
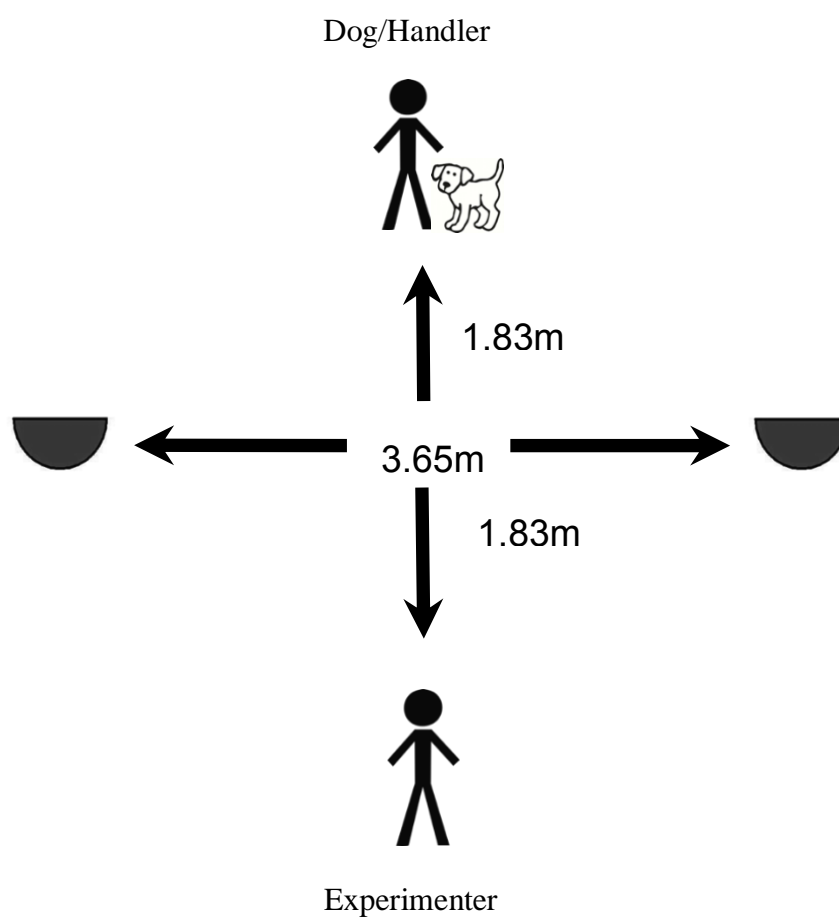
Dog/Handler

1.83m

3.65m

1.83m

Experimenter

Figure 2.1. Illustration of experimental design for Experiment 1.

that bowl. The experimenter then walked over to the other bowl, and dropped pieces of food sequentially into that bowl. The order in which the experimenter approached the bowls was counterbalanced. In the 1 vs 0 condition, the experimenter would drop one piece of food in one of the bowls, and then simply stood for a moment in front of the other bowl. It was not known whether the dogs would pay more attention to the visual cue of the food being dropped into the bowl, or to the auditory cue of the food hitting the bottom of the bowl. Food items were thus chosen based on two criteria a) the food items had to be very desirable to the dog, and b) the food items had to be hard enough to make an audible sound when they hit the bottom of the bowl. This ensured that dogs had access to both visual and auditory cues before making their choice.

In order to control for any cues relating to timing (because it takes longer to drop three pieces of food than one piece of food, the dog could make a correct decision based upon how long the experimenter spent at each bowl), the experimenter spent extra time at the bowl containing less food. For example, on a 4 vs 1 trial, if the experimenter took 4 s to drop four pieces of food in the first bowl, then she spent 1 s dropping a single piece of food in the second bowl and paused for an additional 3 s.

After the food was dropped into each of the bowls, the experimenter returned to her starting position and turned her back to the dog. The owner then released the dog. The importance of avoiding "Clever Hans" cues was explained to owners, and they were directed to look straight ahead and avoid "steering" their dogs to either side. If the dog was obedient enough to hold a sit-stay off lead, then the owner did not touch the dog during the trials. If the dog required a lead, then the owner was directed to hold the lead loosely and straight behind the dog. Once the dog was released by the owner, it was allowed to choose and

consume the contents of one of the two bowls. Once the dog made its selection, the owner

took the dog back to its starting position, while the experimenter collected the food from the

remaining bowl.   Approximately 12-24 trials were conducted per session, depending upon

the dog's motivation level, and each session took approximately 45 min to complete. The

intertrial interval was approximately 45 s. The ratios used in this experiment included 0 vs 1,

1 vs 2, and 2 vs 4 pieces of food. All subjects completed 80 trials. Dogs were tested

primarily at obedience schools, and occasionally at the homes of their owners.

Experiment 1b. The same procedure outlined above was used, but weighted lids

measuring 25 cm x 25 cm were added to the bowls so that the dog would have to exert more

effort by knocking off the lid in order to obtain the food. The only ratio used in this

experiment was 4 vs 2, and all subjects completed 80 trials.

Experiment 1c. This task was identical to Experiment 1a, with the exception that the

bowls were placed farther apart (9.75 m instead of 3.64 m), as another attempt to increase the

amount of effort required by the dogs in making a selection. Ratios of 0 vs 1, 1 vs 4, 1 vs 3,

1 vs 2, 2 vs 4, 2 vs 3, and 3 vs 4 pieces of food were used in this experiment, and all subjects

completed 28 trials.

Experiment 1d. Again, the procedure from Experiment 1a was used, but, in this

experiment, dogs were not given food in the bowls. One potential problem with the task

outlined in Experiment 1a is that (with the exception of a ratio of 1vs 0) any choice the dog

makes is reinforced. For example, faced with a ratio of 4 vs 1, if the dog chooses the bowl

with only one piece of food, the choice is reinforced, even if the dog has made an incorrect

selection. This may not be a problem for a scavenger like the domestic dog—especially

given that we often train them using bits of food for reinforcement. In short, a dog may not

care about getting the majority of food, as long as it gets some food. In this variation on the numerical task, the experimenter dropped non-food items into the bowls (plastic bottle caps). The dog was rewarded with food only if it correctly chose the bowl with the majority of bottlecaps. Ratios used in this experiment included 0 vs 1, 1 vs 3, 1 vs 2, 2 vs 4, and 2 vs 3 bottlecaps, and all of the subjects completed 80 trials

Results

The performance of the dogs across all versions of this experiment is presented in Table 2.1. Only in the 1 vs 0 condition in Experiment 1a, $t(6) = 4.09$, $p < .01$, Experiment 1c (all dogs scored 100%), and Experiment 1d, $t(3) = 3.78$, $p < .05$, were dogs able to choose the bowl with the greater amount of food significantly above chance. In all other ratios, their performance was no better than chance, and, importantly, did not conform to Weber's law. This is best illustrated in the percentage correct across ratios for Experiment 1c (See Figure 2.2). For example, according to Weber's law, 4 vs 1 (a ratio of .25) should have been among the easiest ratios (second only to 0 vs 1) for the dogs to discriminate. Surprisingly, 4 vs 1 was one of the most difficult ratios for the dogs to discriminate , and overall there is no trend in the means suggesting that the performance of the dogs across ratios conformed to Weber's law by showing higher accuracy at lower Small (S)/Large (L) ratios and lower accuracy at higher S/L ratios.

Discussion

A major limitation of Experiment 1 was the low number of trials obtained for each dog. This being said, if the dogs could discriminate number at all, then one would expect that even in failing to differ significantly from chance, the dogs' mean performance across ratios should at least begin to conform to Weber's law—it did not. Nonhuman primate

S/L <u>Ratio</u>

<u>Experiment</u>	<u>0vs1</u>	<u>1vs4</u>	<u>1vs3</u>	<u>1vs2</u>	<u>2vs4</u>	<u>2vs3</u>	<u>3vs4</u>
1a	74%**			53.57%	55.36%		
1b						55%	
1c	100%***	41.67%	63.88%	58.33%	55.56%	44.44%	55.56%
1d	78.13%*		59.83%	65.62%	57.81%	54.69%	

Note: All ratios for which data are not presented were not included in that particular variation of Experiment 1. Asterisks represent instances in which selection of the larger number of food items was significantly above chance (50%).

* = $p < .05$
** = $p < .01$
*** = $p < .001$

Table 2.1. Percentage of Correct Selections Across all Variations of Experiment 1.
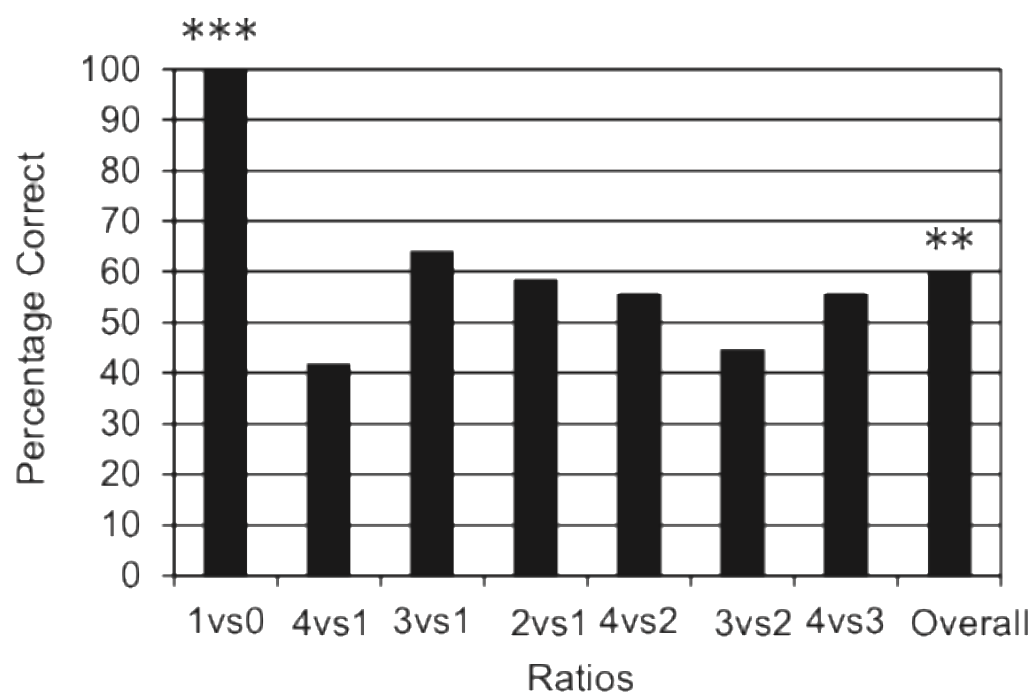
Note: ** = p < .01

*** = p < .005

Figure 2.2. Percentage correct across ratios in Experiment 1c.

tested on this task showed significant preferences and Weber's law effects from the beginning of testing (Beran, 2001; Beran & Beran, 2004). With the exception of the 0 vs 1 ratio, the dogs in this experiment demonstrated no numerical ability.

Zero is not a quantity, but rather the absence of a quantity. The ratio of 0 vs 1 is unique in this experiment in that it is a "food or no food" scenario. There is a possibility that 0 vs 1 was not viewed by the subjects as a numerical task at all. As scavengers, the acquisition of a little more or a little less food may be of little importance to the domestic dog—as long as some food is ultimately obtained. The 0 vs 1 ratio, on the other hand, may be of greater significance because the consequences are more severe—if the dogs choose incorrectly in this case, they receive no food at all.

In all ratios other than 1 vs 0, the dogs received food reward (albeit not the maximum amount available), regardless of the decision they made. While this did not seem to affect performance of chimps in the Beran (2001; Beran & Beran 2004) tasks, it could be more problematic for domestic dogs. All of the subjects in this experiment had undergone basic obedience training, in which they were accustomed to receiving food as positive reinforcement. The fact that they received food regardless of whether they chose correctly or incorrectly could easily have been confusing for the dogs, as they could have perceived any type of food as reinforcement for a correct response.

Another potential issue with the design of Experiment 1 could be the presence of the human experimenter. The experimenter in this task was always in sight of the dog during these trials, and the dog's handler was present in the room as well. Dogs have been intensively bred to pay attention to human beings. It may be very difficult for a dog to

engage in a cognitive task while in the presence of humans, to whom they are strongly inclined to attend.

Dogs have been artificially selected by humans to serve a number of purposes—they have traditionally guarded our homes, herded our livestock, hunted our game, and pulled our sleds. Perhaps, as a result of selecting these animals for a wide range of specific endeavours, we have also systematically "bred out" abilities that would have been more fundamental to the survival of an animal in the wild. Macpherson and Roberts (2006) tested spatial memory in domestic dogs using a signature experimental paradigm—the eight-arm radial maze. Although it was found that much like rats (Olton and Samuelson, 1976) and pigeons (Roberts & Van Veldhuizen, 1989) dogs preferred the use of a win-shift strategy to deplete the maze, the performance of the dogs was quite inferior to that of rats and pigeons (but see Craig et al., 2012). These findings lie in stark opposition to much of the current data from social cognitive studies, in which dogs seem to excel in their interactions with humans. From the age of eight weeks old, a dogs' world is largely dominated by its need to interact successfully with humans. It seems plausible that cognitive functions not directly related to this lifestyle, such as spatial memory or numerical cognition, may simply have been lost or weakened through the process of domestication.

Experiment 2

In all variations of the sequential number task, dogs failed to discriminate numerosity well beyond 1 vs 0. Given the limited number of testing trials per dog in Experiment 1, it was decided to work intensively with a single subject in Experiment 2. Additionally, the task was modified by using simultaneous, rather than sequential presentation of items. Monkeys were able to match numerosity sample stimuli better when they were presented

simultaneously than when they were presented successively (Nieder, Diester, & Tudusciuc, 2006). Perhaps dogs would also show higher accuracy with numerical stimuli presented simultaneously. In this variation of the counting task, a single subject was presented with two boxes. Varying numbers of geometric patterns were affixed to the fronts of the boxes. If the subject correctly chose the box with the greater number of items on the front, it received a reward. If it chose the box with fewer items, it received nothing.

Method

Subject.

Sedona, a one-year-old female rough collie, was the subject of this study. She had no previous experience with this task. Sedona had basic obedience training, and was chosen as the subject of this study simply because she was the pet of the author, and was therefore readily available to participate in the trials. When testing Sedona, her owner did not act as her handler, but baited containers and recorded data, out of Sedona's sight (data were recorded behind Sedona, in the entrance to an adjoining room). Given that the task was not social in nature, and her owner was out of sight, it is not believed that her relationship with the author should have influenced her performance in any way.

Materials.

Two cardboard boxes, each measuring 45 cm x 30 cm x 24 cm, were painted black, and a white magnetic board measuring 35 cm x 28 cm was attached to the front of each box. Numerical stimuli consisted of shapes (large squares, small squares, large triangles, small triangles, large rectangles, and small rectangles) which were cut out of black craft foam and fastened to a magnet. Importantly, all the large shapes had exactly the same amount of surface area (32 cm^2), and all of the small shapes had exactly same amount of surface area

(16 cm^2). Furthermore, all large shapes were exactly twice the surface area of all small shapes. This allowed us to control for the possibility that Sedona was making an area-based decision, rather than a numerically-based decision. For example, in a 2 vs 1 trial, the box with two items would always have more surface area covered than the box with one item, if the items were of equal size. If two small shapes versus one large shape were used, however, the amount of surface area covered by the shapes would be equated. Likewise, with a 6 vs 8 ratio, the surface area of the box occupied by fewer items could actually be made greater on some trials than that of the box with the greater number of items. Also, the configurations of the items on the magnet board were varied randomly from one trial to the next (See Figure 2.3 for examples of these configurations).

The two cardboard boxes each rested on top of a smaller plastic container, measuring 20 cm x 20 cm x 8 cm. These containers were perforated, and contained a false bottom containing food like the bowls in Experiment 1, in order to control for any olfactory cues. In each trial, a single piece of food reward was placed in the container underneath the box with the greater number of shapes attached to the front.

Two cardboard screens, painted grey and measuring 1 m x 1.5 m were also used in these experiments to obscure the two boxes at the beginning of a trial, so that upon entering the room, neither the dog nor the handler could see the boxes. Importantly, the handler kept her eyes shut until the screens were removed and the dog had already made its selection. This additional control was important, as it eliminated any possibility of the handler cueing the dog as to which box contained the food.
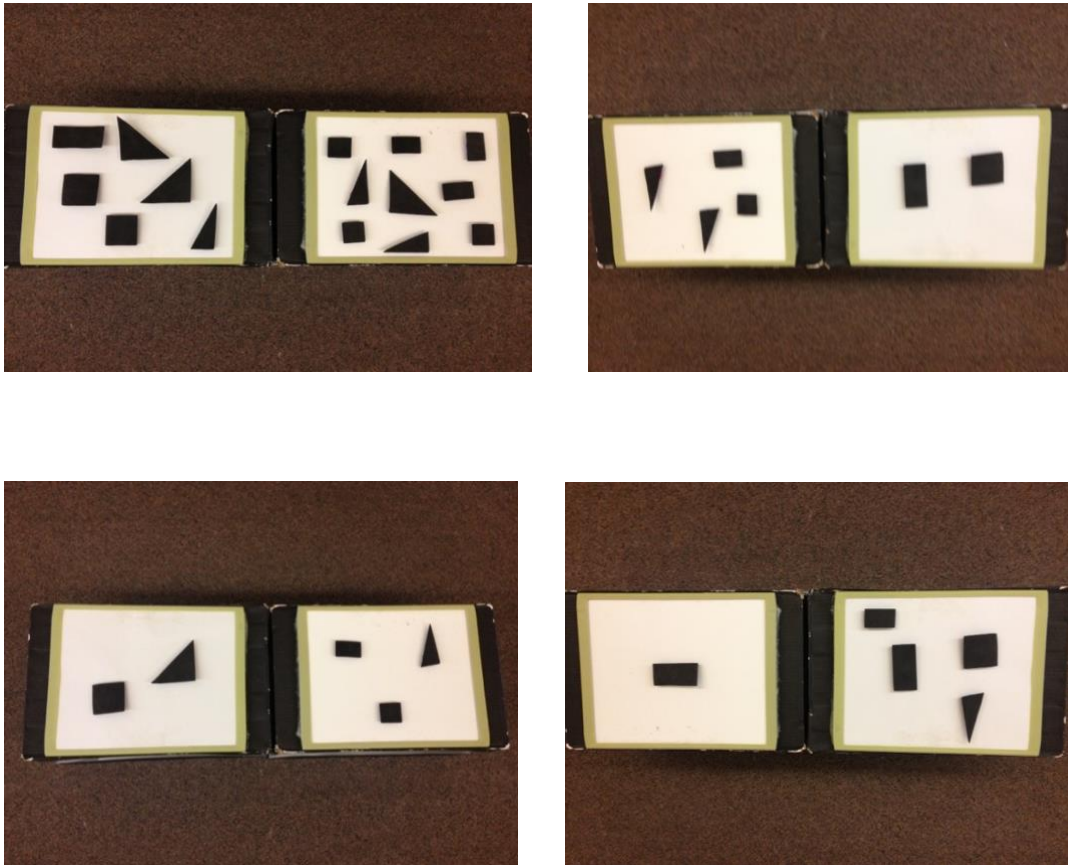
Figure 2.3. Configuration of geometric shapes in order to control for area. In the top left photo, a ratio of 4 vs 2 is shown with equal volume in both sets of items. In the bottom right photo, a ratio of 1 vs 4 is shown with greater volume represented.

Procedure.

On each trial, Sedona was walked into the room by her handler and put in a sit-stay position at a designated spot. At this point, neither Sedona nor her handler could see the boxes, as they were obscured by the cardboard screens. Once Sedona was in position, her handler closed her eyes and said "ready". This cued the experimenter to remove the cardboard screens, revealing the two boxes and the numerical stimuli. The boxes were 1.5 m apart, and Sedona sat 1.2 m away from the midpoint between the two boxes (See Figure 2.4). Once the cardboard screens were removed, the experimenter said "ready" to the handler. Keeping her eyes closed, the handler then mentally counted to four, giving Sedona time to observe the two boxes. The handler then released Sedona with the command "okay", allowing Sedona to choose one of the boxes and knock it over. The handler then retrieved Sedona, while the experimenter picked up the boxes in preparation for the next trial. If Sedona chose correctly, she was allowed to consume the reward found in the container underneath the box. If she chose incorrectly, there was no food available in the container under the box and thus she received no reward.

All testing was done in a single room at the University of Western Ontario. Sedona was tested twice a day, at approximately 10 am and 2 pm, Tuesdays through Fridays. She completed 24 trials per session. There was an intertrial interval of approximately 1 min between trials. Each session took approximately 40 min to complete.

Sedona was initially trained on the ratios of 0 vs 1, 1 vs 4, 1 vs 3, 1 vs 2, and 2 vs 3. The right-left position of the larger-number and smaller-number cues was varied randomly across trials. Sedona was trained on each of these ratios individually until she reached a criterion of 70% on each. She was then formally tested on these ratios mixed, with

Figure 2.4. Sedona making a selection of a box in Experiment 1.

Results

Sedona was initially tested on ratios of 0 vs 1, 1 vs 2, 1 vs 3, 1 vs 4, and 2 vs 3. She

was then tested on all of these ratios, as well as the novel ratio of 1 vs 5. Sedona's

performance was not significantly above chance on the most difficult ratio (2 vs 3), but her

performance was above chance on all other ratios (ts (df) $\geq 2.71, p < .05$). There was a

strong negative correlation between her percentage correct and the S/L (the smaller number

of items divided by the larger number of items) ratio, $r(5) = -.91$, p $< .01$, indicating that

Sedona's performance systematically declined as ratios became larger (See Figure 2.5).

Subsequently, to determine if Sedona's ability would transfer to more difficult novel

ratios, she was tested on ratios of 0 vs 1, 0 vs 3, 1 vs 2, 1 vs 3, 1 vs 9, 2 vs 4, 3 vs 4, 3 vs 9,

4 vs 8, 6 vs 8, 6 vs 9, and 8 vs 9. Data for ratios of the same numerical magnitude (0 vs 1

and 0 vs 3, 3 vs 9 and 1 vs 3, and 4 vs 8, 2 vs 4, and 1 vs 2) were merged for this analysis.

Once again, Sedona's performance was significantly above chance (ts (df) $\geq 2.6, p < .05$), on

all but the most difficult ratio (8 vs 9). The correlation between percentage correct and the

S/L ratio approached significance $r(6) = -.81, p = .053$ (See Figure 2.6a).

When data for the two sets of ratios completed by Sedona were merged, a strong

negative correlation was found between percentage correct and the S/L ratio $r(8) = -.86, p <$

.01 (See Figure 2.6b). Overall, these findings suggest that Sedona was able to discriminate

number, and that her accuracy decreased as the S/L ratio increased, as predicted by Weber's

law.

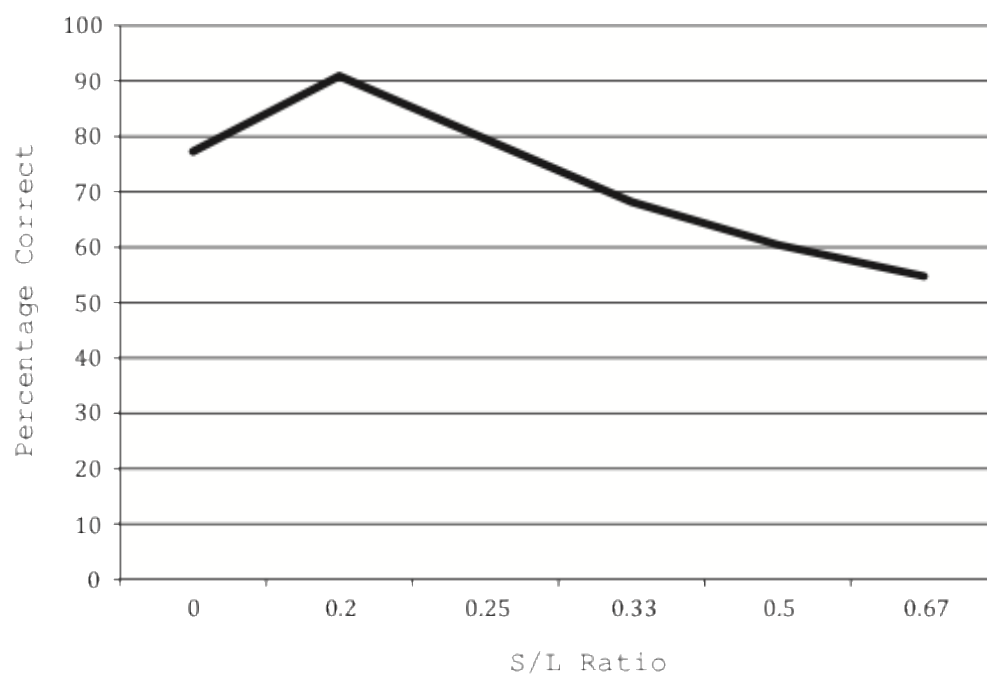*Figure 2.5.* Sedona's initial performance in Experiment 2, with trained ratios of 0 vs 1, 4 vs 1, 3 vs 1, 2 vs 1, and 2 vs 3, and the novel ratio 5 vs 1.
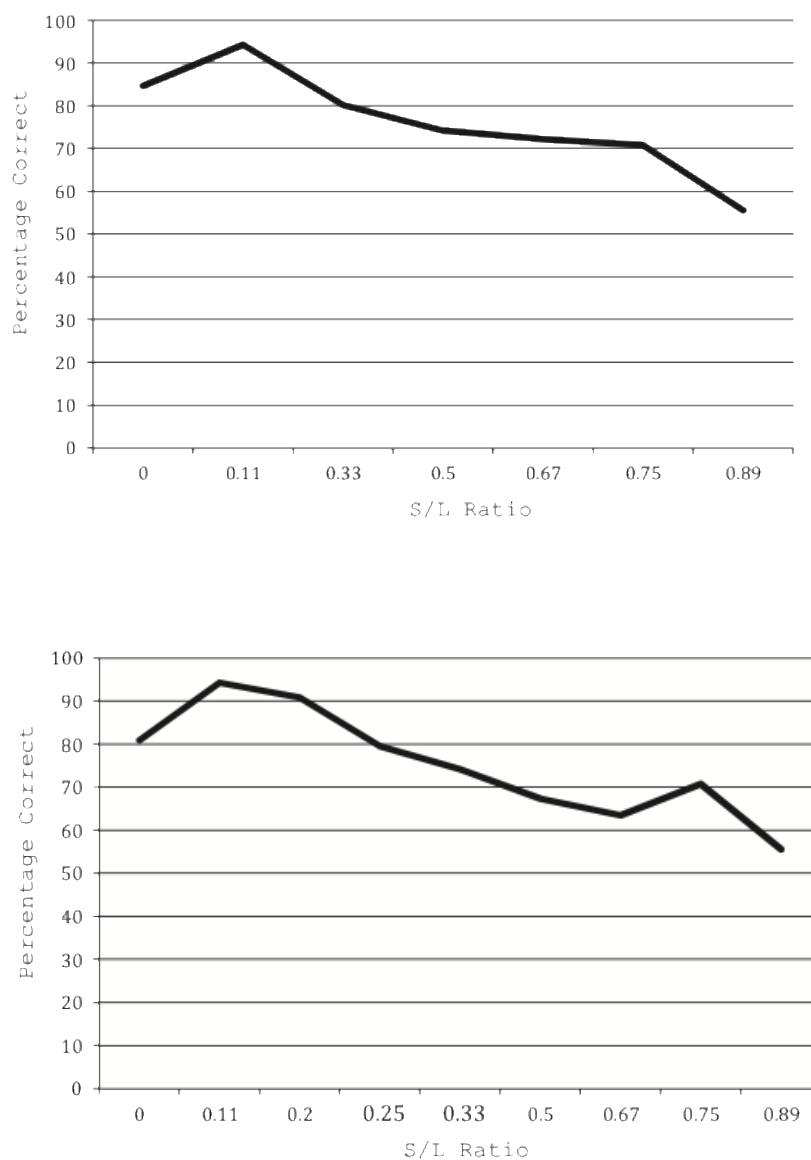
Figure 2.6. (A; Upper Panel) Sedona's final performance in Expeiment2, with ratios of 0 vs 1, 1 vs 3, 1 vs 2, and novel ratios of 0 vs 3, 1 vs 9, 3 vs 9, 4 vs 8, 2 vs 4, 6 vs 9, 3 vs 4, 6 vs 8, and 8 vs 9.

(B; Lower Panel) Combined data for Experiment 2.

Discussion

Although dogs in Experiment 1 demonstrated almost no proficiency in a numerical task, Sedona demonstrated numerical skill that was both above chance performance, and conformed to Weber's law. These findings could be due to a number of factors. An obvious case could be made for the fact that Sedona was tested roughly four days a week and for hundreds of trials, while subjects in Experiment 1 were tested for only a few sessions and received a maximum of 80 trials. Still, if sheer volume of testing were the only explanation for the difference in our findings, it is curious that the mean performance across ratios for the subjects in Experiment 1 did not show any trend consistent with Weber's law. Sedona received considerably more training than the dogs in Experiment 1. This, however, was because Experiment 2 required that she associate the geometric shapes, a non-food item, with subsequent food reward. In Experiment 1, on the other hand, the dogs simply had to count food objects, which should have prompted an innate preference for larger food quantities from the animals.

Experiment 2 removed the possibility of dogs receiving food reinforcement in scenarios where an incorrect choice was made. Additionally, in Experiment 1 the dogs watched as a human experimenter dropped food into each of two buckets, and the experimenter was always in sight of the dog during the trial. Given how intensely dogs have been bred to interact with humans, perhaps the mere presence of the human in Experiment 1 was enough to distract the dog from the task being asked of it. In Experiment 2, on the other hand, the two boxes were presented to Sedona without any interference by the experimenter, and the experimenter was not in Sedona's field of view while she made her selection. This, combined with the fact that she could only obtain food when she made a correct selection,

might have made the procedure in Experiment 2 much more effective for the study of numerosity in dogs.

One notable observation made across the two studies was that there were differences in how the dogs in Experiment 1 observed the trials, versus how Sedona observed her trials. In Experiment 1, dogs tended to lunge randomly at either bowl, and did not appear to spend much time considering the two options available to them. Sedona, on the other hand, very obviously shifted her gaze from one box to other at least once before selecting a box. Tolman (1939) referred to this type of looking behavior as vicarious trial and error (VTE) in rats. Sedona's use of VTE suggests that she was actively engaged in viewing each of the visual stimuli and only subsequently making a choice. Dogs in Experiment 1 did not appear to use VTE, and appeared to make their choices randomly, or simply chose whichever bucket was most directly in their line of sight.

Experiment 1 used sequential presentation of stimuli, whereas Experiment 2 used simultaneous presentation. Nieder et al. (2006) found that sequential and simultaneous enumeration processes engaged different populations of neurons in the intraparietal sulcus of monkeys during a match-to-sample task. Once the enumeration process was completed, another group of neurons represented the cardinality of a set, regardless of whether it had been presented sequentially or simultaneously. Overall, however, the monkeys found stimuli more difficult to discriminate when presented sequentially than when presented simultaneously. Given our current findings, it seems plausible that dogs experience a similar difficulty in the processing of sequential stimuli.

Another issue related to Sedona's success may be her breed. Sedona is a rough collie, a breed traditionally used to herd sheep—a highly visual task. Collies are also descended

from sighthounds, which were bred to track and hunt animals visually. It is from this ancestry that collies obtained their long, lean, head. Studies have shown that topography of the retinal ganglion cells in the eyes of dogs are highly and positively correlated with length of skull (Peichl, 1992; Miller & Murphy, 1995). While short-faced brachycephalic breeds (e.g., pug, bulldog, pekingese) have retinal ganglion cells concentrated in one area centralis, long-faced dolicocephalic breeds (e.g., collie, greyhound, saluki) have their retinal ganglion cells arranged in a long "visual streak", which is more similar to a wolf retina. Gácsi et al. (2009) found that in a two-choice pointing task, dogs with more forward facing eyes actually followed the point better than dolichocephalic breeds. Based on these findings, Sedona should have actually been at a disadvantage in this task, relative to a brachycephalic breed. It is important to remember that although we often tend to insist upon testing animals in the visual paradigms that we as humans are comfortable with, the dog is not really a visual animal—their world is undoubtedly better navigated through olfaction. Part of Sedona's success in this task then could be related to the fact that she is of a breed that is more inclined to attend to visual information. A number of the dogs in Experiment 1 were of sporting and scent hound origin; these breeds would likely be more scent driven, and may be less inclined to attend to visual stimuli. This would constitute a perceptual, and not cognitive, difference in breeds that could be of great practical importance, considering the current boom of dog cognition studies being published.

General Discussion

Overall, our findings provide an interesting insight into the numerical ability of domestic dogs. In Experiment 1, we found no evidence of numerical ability outside of a 1 vs 0 scenario, and performance of the dogs across ratios failed to conform to Weber's law. In

Experiment 2, on the other hand, we found compelling use of numerical ability in a single subject across a large number of S/L ratios. Because Sedona was able to discriminate S/L ratios that fell well above the range of 1-4 items, and because her performance was ratio-dependent, there is no evidence that she is confined to an object file system (Carey, 1998; Feigenson, Dehaene, & Spelke, 2004). Rather, Sedona's performance is consistant with predications made by the ANS (Merritt, DeWind, & Brannon, 2012).

The reasons for Sedona's success in Experiment 2 could be related to a number of factors. Experiment 1 used a sequential presentation strategy, while Experiment 2 used simultaneous presentation. Sedona also had the benefit of having far more trials and being tested much more consistently. Breed differences are also potentially an explanation for our findings and should be carefully considered in future studies.

Sequential presentation in a numerical task with dogs should be revisited, in order to determine whether or not dogs can discriminate number in this presentation modality. It is not known at this point whether the dogs in Experiment 1 could have discriminated numerosity if they had been given simultaneous presentation, or whether Sedona would have performed as well as she did in a task using sequential presentation. These questions will be addressed in future studies.

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Chapter 3

On the Clock: Interval Timing and Overshadowing in Domestic Dogs *(Canis familiaris)*

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Abstract

Interval timing is an important skill that allows animals to approximate how much time has elapsed since a given event. Little, however, is known about interval timing in domestic dogs. In an initial experiment, dogs were trained to make an operant response on a fixed interval 30-s schedule, with either a light or a tone + light compound signalling the beginning of each fixed interval. When dogs in the compound group were subsequently tested with 60-s tone-only probe trials, the dogs' rate of responding peaked near 30 s. When the same dogs were tested with light-only probes, however, no evidence of timing was found. In a second experiment, a bi-section task was used in which dogs had to learn to approach one feeder when given an 8-s tone + light signal, and another feeder when given a 2-s tone + light signal. When subsequently tested at intermediate durations, psychophysical curves showed clear control of timing by the tone stimulus but not by the light stimulus. These findings demonstrate clearly that dogs are able to time fixed intervals and show the existence of an overshadowing effect, in which dogs are able to time a light cue presented alone but do not attend to the light when it is presented simultaneously with a tone.

Keywords: interval timing, peak procedure, overshadowing, dogs

On the Clock: Interval Timing and Overshadowing in Domestic dogs (*Canis familiaris*)

A number of species have demonstrated the ability to keep track of both time of day (circadian timing) and the durations of time intervals (Vasconcelos, de Carvalho, &Machado, 2017). The evolutionary advantage circadian timing conveys is the ability to estimate the time of day when prey, mates, or predators may be found at a particular location (Biebach, Gordijn, & Krebs, 1989; Wilkie et al., 1996). Interval timing allows animals to forage efficiently by accurately estimating the travel time between different food locations, the handling time of prey, and the time needed to reach cover in case a predator arrives (Lima, 1984; Stephens & Krebs, 1986).

Interval timing has been studied in a wide variety of species, including bumblebees (Boisvert & Sherry, 2006), wasps (Schmidt & Pak, 1991), fish (Higa & Simm, 2004), hummingbirds (Henderson, Hurly, Bateson, & Healy, 2006), hens (Taylor, Haskell, Appleby, & Waran, 2002), pigeons (W. Roberts, Cheng, & Cohen, 1989), turtle doves (Lejeune & Richelle, 1982), rats (S. Roberts, 1981), possums (Sargisson, Lockhart, McEwan, & Bizo, 2016), and humans (Wearden & McShane, 1988). In the fixed interval (FI) procedure, only a response made after the expiration of a fixed interval of time, measured from the last reinforced response, or from the onset of a signal, are reinforced. Accuracy of FI timing is indicated by the how long an animal waits or responds at a low level before accelerating its rate of responding as the end of the FI approaches. In a modification of the FI procedure, the peak procedure (S. Roberts, 1981), FI training is followed by probe trials that last longer than the FI with no responses reinforced. Plots of the mean number of responses made at successive time intervals during probe trials yield approximate Gaussian curves that peak

near the end of the fixed interval. Both FI curves and peak-time curves indicate accurate timing in a number of species.

Although several theories of timing have been proposed (Crystal & Baramidze, 2007; Killeen & Fetterman, 1993), the most influential account of timing remains the information processing model proposed by Gibbon (1977; see also Gibbon, Church, & Meck, 1984). Known as Scalar Expectancy Theory (SET), this model theorizes three main components, which constitute an internal timing system: the pacemaker, an accumulator, and a switch. According to the SET model, time is tracked through internal pulses emitted by the pacemaker at a consistent rate. The pulses are then collected by the accumulator. While the pacemaker emits pulses continuously, the accumulator is started and stopped by a "switch", which allows information about specific durations to be processed. Once the event being timed has been completed, information (i.e., the number of pulses generated) is gathered from the accumulator, and stored in working memory. While in working memory, the number of pulses is compared to a sample drawn from previous durations stored in reference memory. Comparisons are then made in order to determine whether the interval is shorter or longer than the previously-encountered example. Thus, an animal tracking a 30-s FI would begin to respond rapidly once the pulses in its accumulator approached a comparison number drawn from reference memory.

According to SET, the timing process is ratio dependent, which means that it obeys Weber's law. Thus timing becomes less precise as durations to be timed get longer. SET theory predicts *scalar invariance*, meaning that error in timing an interval will be proportional to its duration. The precision of timing has been estimated by the coefficient of variation (CV), the standard deviation of a timing curve divided by the peak or FI. Narrow

curves suggesting onset and offset of responding near the peak of the curve then yield smaller CVs than broader curves at the same fixed interval of time.

In a comparative review of interval timing, Lejeune and Wearden (1991) found that in a number of species, the CV increased as the duration of FIs increased. They attributed this increase to the influence of responding based on non-timing processes. At shorter FI durations (less than 100 s), comparisons across species showed that CVs increased from lowest in cats and monkeys (≈ 0.2) to rats and mice (≈ 0.3), pigeons (≈ 0.4), and highest in freshwater turtles (≈ 0.6). In a study of the production of short time intervals (0.5-1.3 s), Wearden and McShane (1988) found that human CVs ranged from 0.11 to 0.14.

Studies of Dog Cognition

Cognitive studies of the domestic dog are currently seeing their heyday—over the past 20 years, study of the domestic dog in psychology has seen exponential growth. While historically dogs were viewed as an "artificial" species due to their domestication (Miklósi, 2015), current research now argues that their unique relationship with humans is precisely what makes the domestic dog a worthy topic of study. As a result, the vast majority of research in dog cognition has focused on various aspects of social cognition. These studies include performance in detour tasks (Frank & Frank, 1982; Pongrácz et al., 2001), the use of human pointing cues to infer directionality (Hare, Brown, Williamson, & Tomasello, 2002; Soproni, Miklósi, Topál, & Csányi, 2002; Udell, Dorey, & Wynne, 2008), and studies of attachment between dogs and humans (Nagasawa et al., 2015; Prato-Previde, Custance, Spiezio & Sabatini, 2003; Topál, Miklósi, Csányi, & Dóka, 1998; Topál et al., 2005). Elements of language have also been examined in these studies—two border collies, Rico (Kaminski, Call, & Fischer, 2004) and Chaser (Pilley & Reid 2011), successfully learned the

names of 200 and 1022 objects, respectively. Chaser, additionally, demonstrates use of word order that is consistent with an understanding of syntax (Pilley, 2013).

What appears to be lacking in the dog literature is an understanding of basic cognitive processes, including the ability to track time. Many dog owners offer anecdotal accounts of their dogs "knowing" what time it is, either by pawing at their food bowl around dinner time, or by pacing at the door when they anticipate the arrival of an owner returning home from work. While it is entirely possible that dogs are in fact keeping track of time in these scenarios, it is also quite possible that external cues (e.g. the owner approaching the food bin, or the sound of a familiar car approaching the home) are what tip off the dogs in these anecdotes. Another possibility is that dogs may be using interval timing based on external cues. Given how intensely dogs have been selected by humans to perform certain tasks, it is important that it is not simply assumed that dogs are sensitive to time in the way that has been demonstrated with other non-human animals. It seems entirely possible that as we have bred them to be our companions, we have "bred out" other traits, such as an ability to track time, which might have been important to their wild ancestors (Frank, 1980).

With the notable exception of Pavlov's (1927) work in classical conditioning in dogs (where time was examined in terms of the duration between the presentation of the conditioned and unconditioned stimuli), almost nothing is known about sensitivity to time intervals in the domestic dog. At the time of this writing, no empirical papers on interval timing in dogs could be found in any peer-reviewed academic journals. Some scientific data suggesting that dogs may be sensitive to time of day was provided by V.S. Rusinov (1973), a Russian scientist who used dogs to study electrophysiology of the brain. Each day, Rusinov's lab conducted training for perceptual experiments—dogs were tested five days a

week, at the same time every day. When dogs initially came into the lab, brain waves showed that the dogs were fairly relaxed. Once testing started, however, brain wave patterns began to show activity consistent with arousal. In one published account (Coren, 2004), Rusinov unexpectedly brought a group of visitors to the lab on a weekend for a tour. To his surprise, a dog which was regularly scheduled to be tested at that time showed the increased activation patterns. Once the dog's testing time had passed, however, its brain activity returned to its resting state. Though anecdotal, Rusinov's observations suggest that dogs are highly sensitive to time of day.

That dogs are sensitive to intervals of time was suggested by Pavlov's (1927) experiments on delay conditioning. In these experiments, the time interval between the presentation of the conditioned stimulus (CS) and the presentation of the unconditioned stimulus (US) was gradually lengthened. It was found that dogs' salivary conditioned response was inhibited during the extended delay and only appeared near the time when the unconditioned stimulus was scheduled to be delivered. Although Pavlov interpreted this finding as a manifestation of the process of internal inhibition, delay conditioning may be seen as a Pavlovian form of interval timing, similar to that seen in more recent operant conditioning studies using fixed intervals and the peak procedure (S. Roberts, 1981).

The Overshadowing Effect

Pavlov (1927) was the first to report the overshadowing effect: if two stimuli are presented at the same time, the presence of the more-salient stimulus may impede learning about the less-salient stimulus. In a series of experiments, Pavlov used several types of compound stimuli to demonstrate overshadowing of one stimulus by another. In one case, a conditioned reflex was established to the simultaneous use of a tone emitted via a tuning fork

and a visual stimulus consisting of three electric lamps. Both stimuli were presented in front of a dog in a slightly-shaded room and followed by food reinforcement . After a dog developed a clear salivary response to the tone-light compound, each component was tested alone. A clear overshadowing effect was found, such that the tone alone produced salivation but the lamp alone did not produce salivation. The sound produced from the tuning fork appeared to have overshadowed the lamp as a cue.

Overshadowing is often described as a competition between stimuli. The Rescorla-Wagner (1972) model, for example, posits that there is a limit to the associative strength that may be conditioned by any given reinforcer, and this fixed amount must be shared between all CSs present on any trial. Theories of selective attention (Sutherland & Mackintosh, 1971), on the other hand, hold that conditioning requires that the subject attend to the CS and that there is an inverse relationship between the strengths of attention to different stimuli. Both theories provide potential explanations of overshadowing--if one component of a compound CS is more salient than the other, it will capture the major share of attention or associative strength and will thus prevent conditioning to the other component.

Experiment 1

The goal of Experiment 1 was to determine whether dogs could, in fact, time fixed intervals. Given that the standard apparatus typically used in timing studies (i.e., the operant conditioning chamber with keys for pigeons and levers for rats) are quite small and enclosed, a new apparatus was developed for use specifically with dogs. This apparatus involved making modifications to an existing commercial treat dispensing device for dogs, known as the Manners Minder ™. Once modified, this apparatus included a button that the dogs were

trained to hit with their paws in order to make an operant response and potentially receive a food reinforcer from the apparatus.

Initially, dogs were trained simply to hit a button for food reward. Once this behavior was acquired, a 30-s FI was imposed. The dogs were free to press the button as much as they wanted, but the feeder was not armed until 30 s had elapsed. The dogs could receive a reward for the first button press response they made after 30 s. Importantly, the onset of these 30-s intervals was signaled for different groups of dogs by either a compound stimulus consisting of both tone and white light or by a white light alone. This procedure allowed us to examine the salience of these different types of cues for dogs, and also allowed us to test for the possibility of an overshadowing effect. A tone-alone training condition was not used because we were primarily interested in seeing whether a tone stimulus would overshadow a light stimulus in a timing task, as seen by Pavlov (1927) in his studies of dog salivary conditioning. Once dogs showed response curves indicating sensitivity to the 30-s FI, occasional nonreinforced 60-s probes were also given to the dogs. These 60-s probe trials were used to generate curves showing responding during and beyond the FI duration (S. Roberts, 1981). In rats and pigeons, a peak time curve is typically seen with responding being maximal near the FI and dwindling at times shorter or longer than the FI, creating an approximation to a Gaussian curve (S. Roberts, 1981; W. Roberts et al., 1989). In the experiment reported here, probe trials were conducted using light, tone, and tone + light compound stimuli.

Method

Subjects.

Subjects were six dogs of differing breeds. All dogs were between the ages of 2 and 5 years (mean age = 3.8 years). The subjects included Cash, a male rough collie, Kip, a male mixed breed, Pepper, an Australian cattle dog, Harriet, a female löwchen, and Ruby and Lucy, both female Labrador retrievers. All dogs were pet dogs who were volunteered for the study by their owners. All dogs had received basic obedience training and were in good health with vaccines in good standing.

It should be noted that Cash belongs to the author of this paper. As such, it was ensured that Cash was never handled by his owner while being tested, although she did at times record data by standing behind him, out of his sight. Given that this task is not social in nature, and his owner was out of sight, it is not believed that Cash's relationship with the author in any way influenced his performance on this task.

Apparatus.

Our apparatus involved making modifications to an existing device—the commercially available Manners Minder™ reward delivery system (Figure 3.1). The Manners Minder device measured 34 cm x 20.8 cm x 19.0 cm. Using a remote control, the Manners Minder can be used to dispense rewards, one at a time, for pet dogs. For our purposes, we secured a Manners Minder to a wooden platform (measuring 61.0 cm x 50.2 cm) and mounted an additional square button (measuring 8.8 cm x 8.8 cm) to the platform. This button was wired to the Manners Minder such that when dogs pressed the button, a
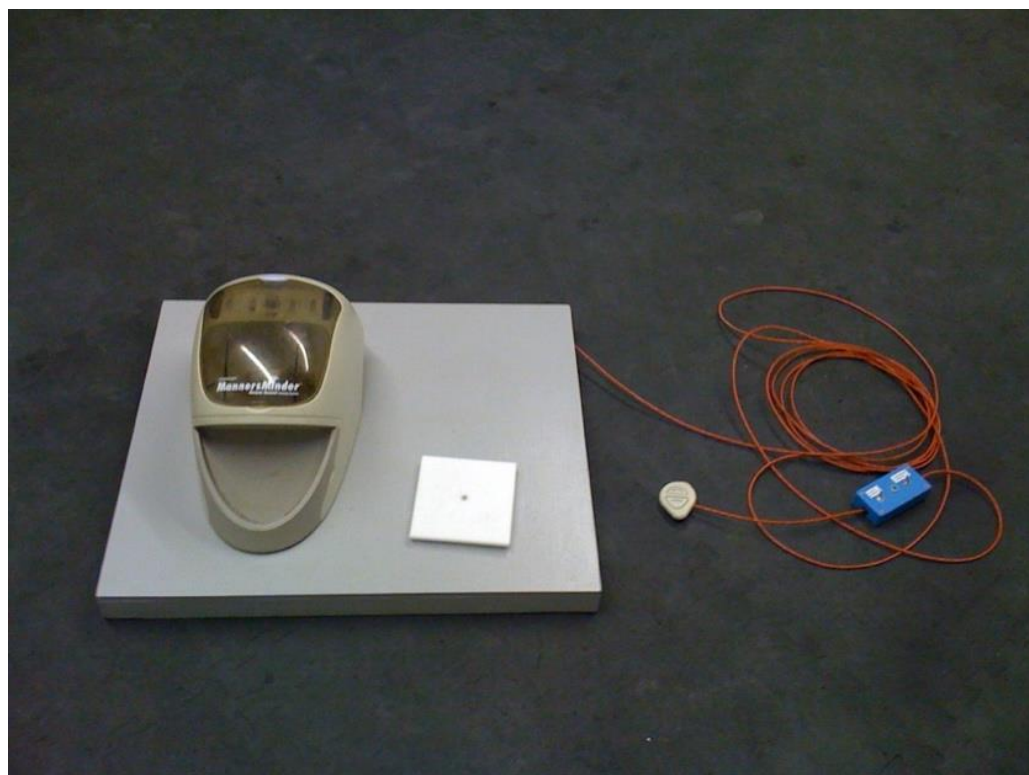
Figure 3.1. Modified Manners Minder apparatus used for Experiments 1. Two of these devices were used in Experiment 2.

reward could be either dispensed or not dispensed (this was controlled by an additional remote control panel). Functionally, this apparatus is analogous to operant conditioning chambers typically used in interval timing studies with pigeons and rats. That is, the device operates such that when a dog makes an instrumental response (pressing the button), food is automatically dispensed from a feeder. Rewards dispensed by the feeder were either bacon-flavored sucrose pellets, or Zuke's® brand dog treats, depending on the taste preference and dietary needs of the dog being tested.

In addition to the Manners Minder apparatus, a small control box (measuring 13.3 cm x 10.1 cm x 5.3 cm) was used to present either the light, tone, or compound stimuli (Figure 3.2). The tone had a frequency of 2800 Hz and an intensity of 78 dB, and a 4-W lightbulb was used to emit the white light signal. The duration and type of stimuli were controlled using switches on the box, and the signal was started using a trigger button, which was attached to the box via a long cord, and held in hand by the experimenter. The signal box was placed directly in front of the Manners Minder, making both light and tone signals highly salient to the dog. Dogs were tested in an empty classroom at Western University. The testing room, which measured 13.7 m x 8.5 m, was darkened, in order to make the white light signal highly salient to the dogs. The room was backlit with a small lamp, providing just enough light for the experimenters to see and adjust the controls on the apparatus.

Procedure.

Two experimenters were present at all times during testing. One experimenter handled the subject, while the second experimenter recorded data and controlled the apparatus. Based on random assignment, three dogs (Cash, Kip, and Harriet) were assigned to the compound stimulus (tone + light) group, and the other three dogs (Pepper, Ruby, and
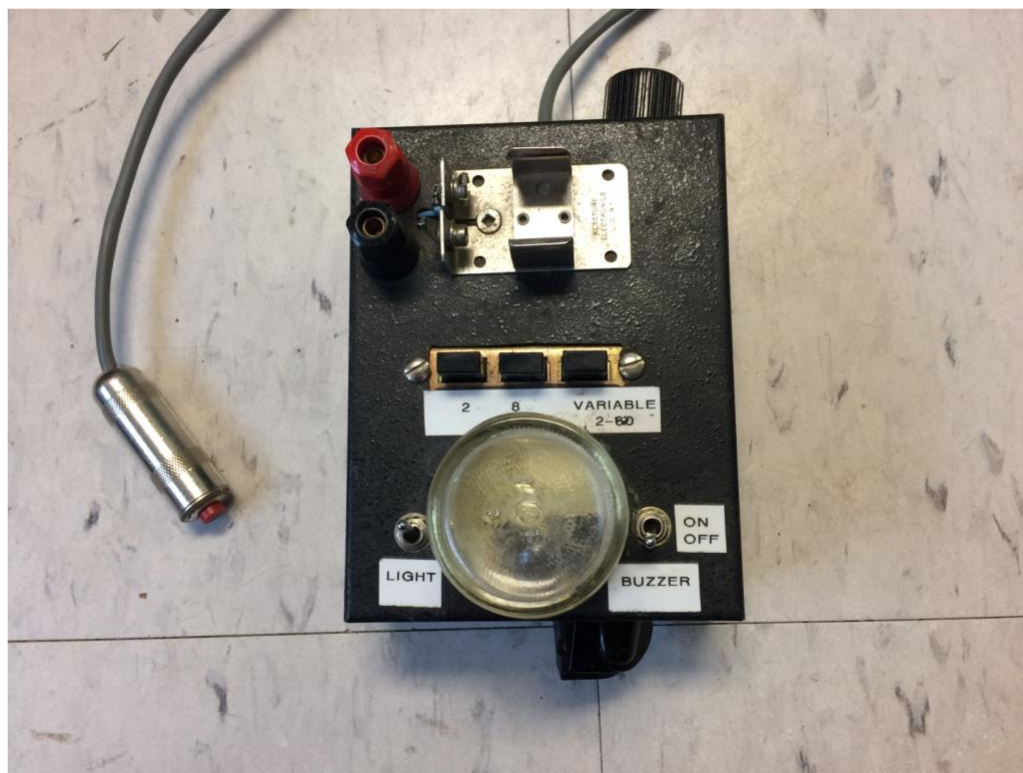
Figure 3.2. Stimulus box used to emit light and tone cues of varying intervals in Experiments 1 and 2.

Lucy) were assigned to the light-only control group. Dogs were first shaped to make the instrumental response, initially receiving a reinforcement for every successful button press. Dogs then received between 20-60 pre-training trials, in which the Manners minder did not deliver a food reinforcer until a button press had been made at least 30 s after the last food reinforcer delivery. During these pre-training trials, the experimenters actively engaged with the dogs, encouraging them to press the button. Encouragement was used to prevent the button-pressing response from extinguishing once a delay in reinforcement was introduced and to prevent the dogs from becoming frustrated with the task. Some dogs were not available as regularly as others, which resulted in more training trials being needed for these dogs to acquire the task. Pre-training was complete when a dog consistently engaged in button pressing.

Once pre-training was completed, an FI 30-s schedule of reinforcement was imposed. A trial began when either a light alone (light-only group) or a tone + light compound (compound group) was presented, and only the first button press made after 30 s had passed was rewarded. The dog was held in place 0.5 m in front of the feeder by Experimenter 1 (this distance was indicated to the experimenters by a mark on the floor), who released the dog when the trial began. Both Experimenters 1 and 2 stood behind the dog and the apparatus and did not touch the dog during the duration of the trial, thus eliminating the possibility of the dog using gaze cues or otherwise being influenced by the experimenters. The number of button presses and times at which button presses were made were recorded using a stopwatch application on a smart phone by Experimenter 2. Dogs were trained for approximately 20 trials in each session (some dogs received slightly more or fewer trials depending upon their motivation to engage in the task). Training on the FI 30-s schedule was

judged to be completed when a dog showed a low level of responding during the initial 5 s of the FI followed by an increasing rate of responding up to 30 s.

After FI training was completed, 60-s nonreinforced probe trials were introduced and were randomly dispersed among the usual 30-s FI training trials. In a single session, a dog received 20 FI training trials and two 60-s probe trials. Dogs in the compound group received 60-s nonreinforced probe trials on different sessions in which the tone-light compound was presented, the tone alone was presented, or the light alone was presented. Dogs in the light-only group received only light probes. The number of probe trials given varied between 15-25 for each stimulus or the compound, depending on a dog's availability for testing. Thus, the dogs trained with the compound tone + light stimulus received about three times as many probe trials as the dogs trained with the light alone. Dogs were typically tested 2-3 times per week, depending on the dog's availability. Testing sessions lasted approximately 40 min.

Results

The three dogs in the light + tone compound group learned to time this signal in 31, 33, and 46 trials, respectively ($M = 36.67$). The three dogs trained with light alone took longer to learn to time this signal, 77, 89, and 129 trials, respectively ($M = 95.33$). The development of FI 30-s responding is shown for each dog in the compound (tone + light) group in Figure 3.3. These curves plot the mean number of responses made during successive 5-s intervals within trials. Curves are shown for early, middle, and late training trials for each dog but vary in the total number of trials, as dogs required different amounts of training. It can be seen that the dogs varied in their rates of responding. Harriet responded at a very high rate on the initial 10 trials and then reduced responding on later trials. A similar
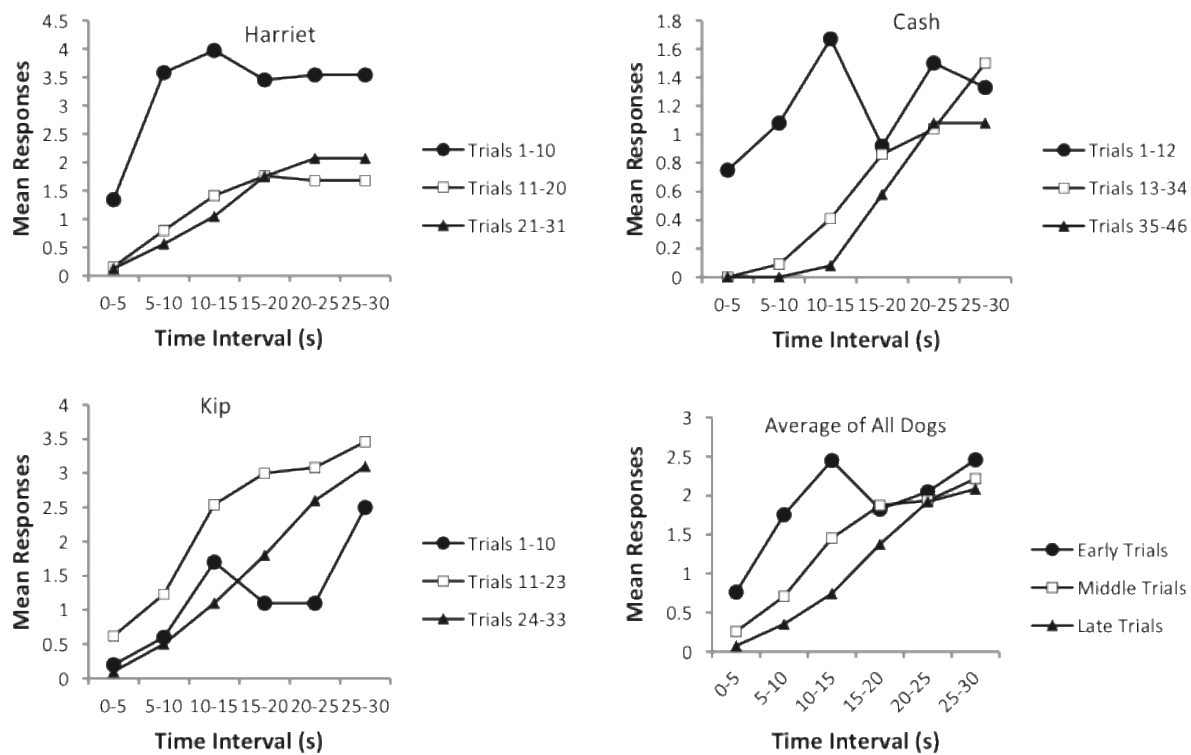
Figure 3.3. Acquisition of responding on an FI 30-s schedule by three dogs in the compound stimulus (tone + light) group.on an FI 30-s schedule by three dogs in the compound stimulus (tone + light) group.

pattern is seen for Cash, although his overall rate of responding is lower. Kip, on the other hand, showed a lower rate of initial responding. Most importantly, all of the dogs show an FI curve on late trials in which responding is low during the early time intervals and gradually increases to the highest level of responding in the final 5-10 s.

A block of trials (early, middle, and late) x six time intervals analysis of variance (ANOVA) performed on these data revealed significant effects of time interval, $F(5, 10) = 11.24$. $p < .01$, $\eta_p^2 = .85$, and a block of trials x time interval interaction, $F(10, 20) = 4.60$, $p < .01$, $\eta_p^2 = .70$.

The FI 30-s curves for the three dogs trained with the light only cue are shown in Figure 3.4. Levels of responding again varied among dogs. Ruby and Lucy responded at higher rates than Pepper. However, as with dogs in the tone + light group, responding on the FI 30-s schedule became sharper over trials, with a decrease in responding at the early time intervals and an increase in responding at the later intervals, with the highest level of responding during the 25-30-s interval. A block of trials x time interval ANOVA performed on the data for all dogs showed a significant effect of time interval, $F(5, 10) = 6.13$, $p < .01$, $\eta_p^2 = .75$, and a nonsignificant interaction of block of trials x time interval, $F(10, 20) = .89$, $\eta_\rho^2 = .31$.

Curves showing responding at successive 5-s intervals during 60-s probe trials are presented for individual dogs in the compound group in Figure 3.5. The most striking aspect of these curves is that all three dogs showed a rising curve with peak responding around 30 s and a subsequent decline in responding when either the compound or the tone probe was presented. This pattern is most pronounced for Cash and Kip. Harriet showed more of a plateau of responding between 10 and 40 s but then showed a decline in responding
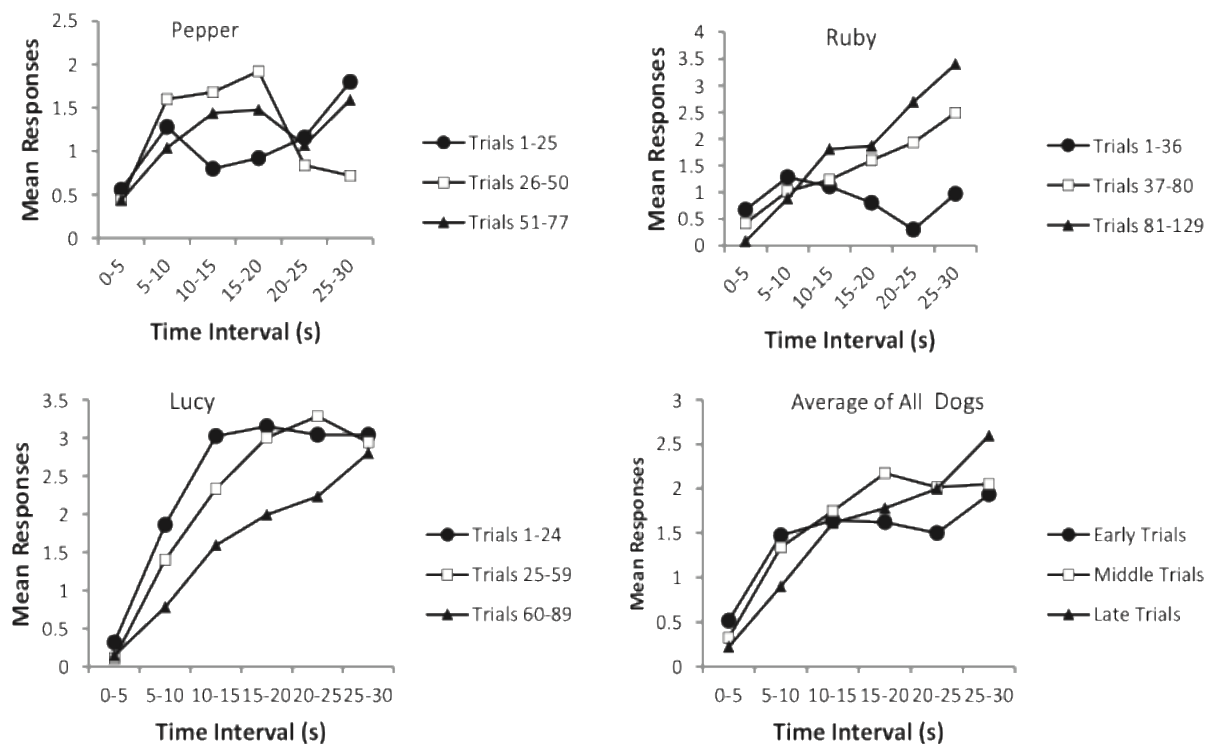
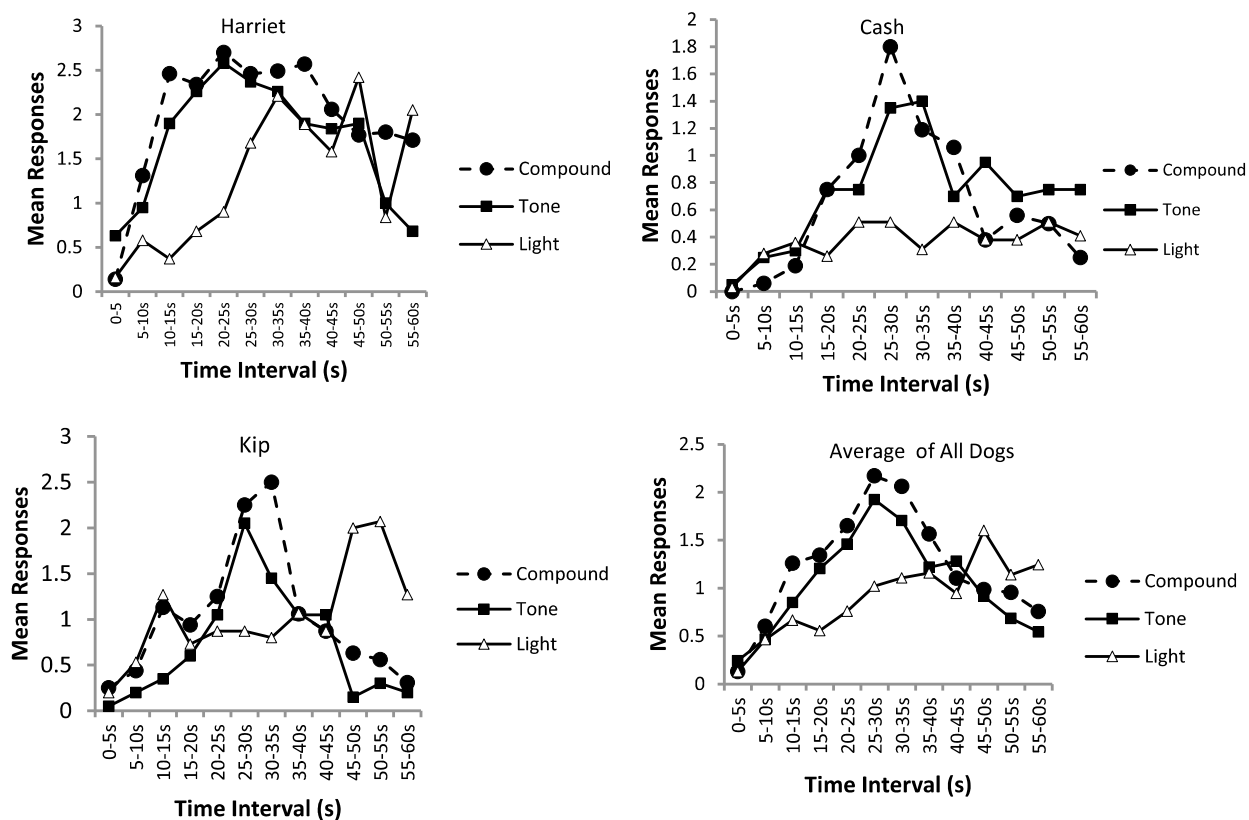*Figure 3.4.* Acquisition of responding on an FI 30-s schedule by three dogs in the light-only group.

Figure 5. Responding by dogs in the compound FI 30-s group to 60-s probes of tone + light (compound), tone alone, and light alon

over the final 20 s. By contrast, responding to the light probe was erratic. Cash showed a fairly flat low level of responding to the light cue. Harriet and Kip showed a rise in responding over the 60-s probe interval but tended to maximize responding toward the end of 60 s.

A 3 (Cue: compound, tone, light) × 12 (Time blocks of 5 s) repeated measures ANOVA assessed the impact of the type of cue used across the 60-s probes. No main effect of cue was found, $F(2, 4) = 1.26$, $p = .38$, $\eta_p^2 = .39$. That is, overall responding to the different cues used did not differ. A main effect of time interval emerged, however, such that more overall button presses were made during the middle of the 60-s probes, $F(11,22) = 12.62$, $p < .01$, $\eta_p^2 = .86$. Most importantly, the interaction of probe cue and time interval was significant, $F(22, 44) = 1.93$, $p < .03$, $\eta_p^2 = .49$, specifically indicating that the mean number of button presses increased and decreased across blocks of time in the compound and tone conditions, but not in the light condition (See panel for average of all dogs in Figure 3.5).

The mid-point of the 5-s time interval in which a dog made the greatest number of responses was used to estimate its peak response time to each probe cue. For the compound cue, the tone cue, and the light cue, the peak time, respectively, was 37.5 s, 27.5 s, and 47.5 s for Harriet, 32.5 s, 32.5 s, and 52.5 s for Cash, and 32.5 s, 27.5 s, and 52.5 s for Kip. The mean peak times for the compound, tone and light cues, respectively, were 34.17 s, 29.17 s, and 50.83 s. A one-way ANOVA performed across these means revealed a significant effect of cue, $F(1, 2) = 25.0$, $p < .05$, $\eta_p^2 = .93$.   Single sample t-tests were also conducted in which the mean of the highest peak was compared against 30 s for each cue. The tests for compound, $t(2) = 2.50$, and tone, $t(2) = .50$, were not significant, but the test for light, $t(2) = 12.5$, $p < .05$, was significant.

The curves in Figure 3.6 show the performance of dogs in the light only control group when tested with 60-s light probes. Both Ruby and Pepper show a peak at the 25-30-s interval, whereas Lucy shows a plateau of responding between 25 and 35 s. The mean for all dogs clearly shows a peak-time curve that peaks at the 25-30s interval. The mean of the midpoint of the peak interval for all three dogs was 27.5 s. A one-way ANOVA used to assess peak time across blocks of time for the three control subjects revealed a significant effect of time interval, $F(11, 22) = 8.81$, $p < .01$, $\eta_p^2 = .82$.

The panel showing average performance for all dogs in Figure 3.6 also shows the mean curve for light probes in the compound group from Figure 3.5. The difference in the shapes of these curves is striking and suggests strong control of responding by time in the light control group and a near absence of control by time when the light cue is presented in the compound group. A group x time interval ANOVA performed on these data yielded significant effects of time interval, $F(11, 44) = 7.76$. $p < .01$, $\eta_p^2 = .66$, and of the group x time interval interaction, $F(11, 44) = 3.58$. $p < .01$, $\eta_p^2 = .47$. The mean peak time of the light only control group (27.5 s) and that of the compound group on light probe trials (50.83 s) differed significantly, $t(4) = 14.0$, $p < .05$.

In Figure 3.7, separate panels show the relative rates of responding on probe trials when dogs were tested with the light-tone compound, the tone alone, and the light in the control group trained with the light alone. Gaussian curves were fitted to these data, with the best fit for the tone alone data ($R^2 = .92$), the next best fit for the light-tone compound data ($R^2 = .85$), and the worst fit for the light alone data ($R^2 = .74$). The CVs for the fitted curves were similar, being .37 for the compound, .36 for the tone, and .35 for the light, indicating little difference in variability across modalities.
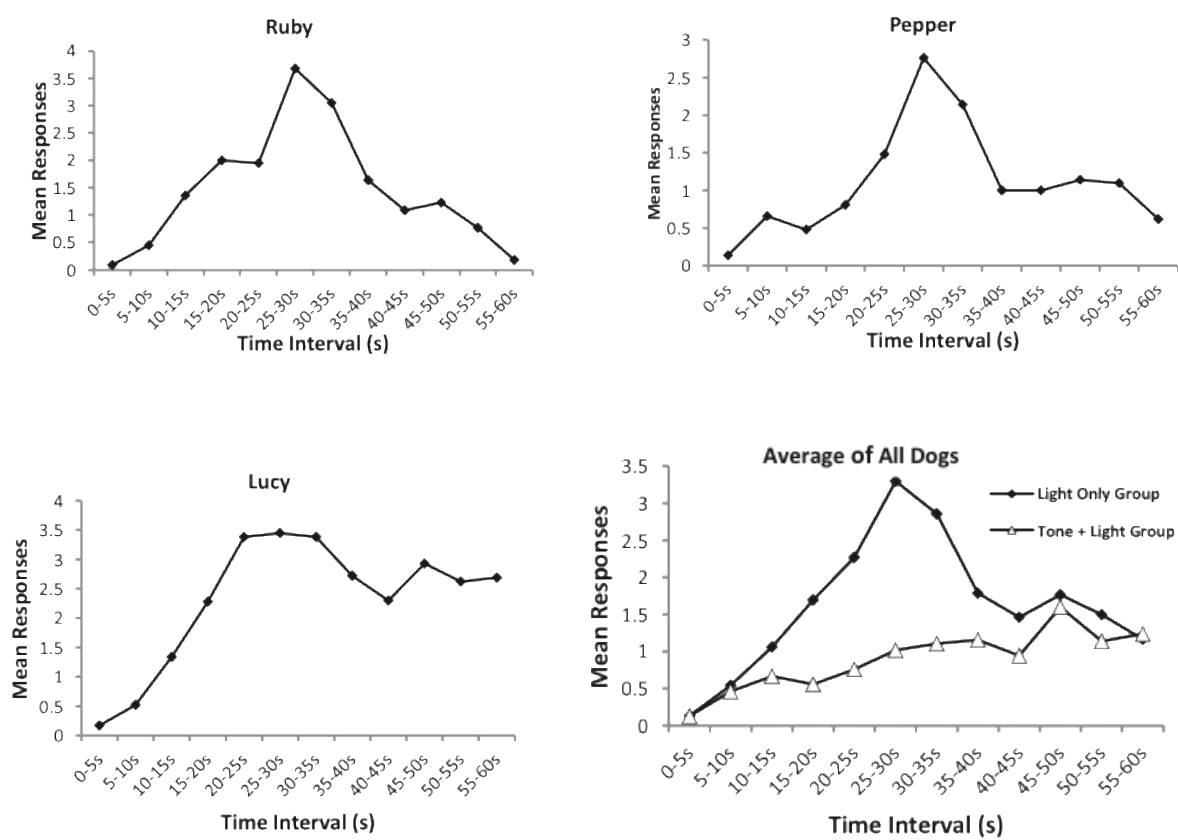
Figure 6. Responding by dogs in the light-only FI 30-s group to light 60-s probes. The average panel shows the curve for light probes in the compound (Tone + Light) group for comparison.
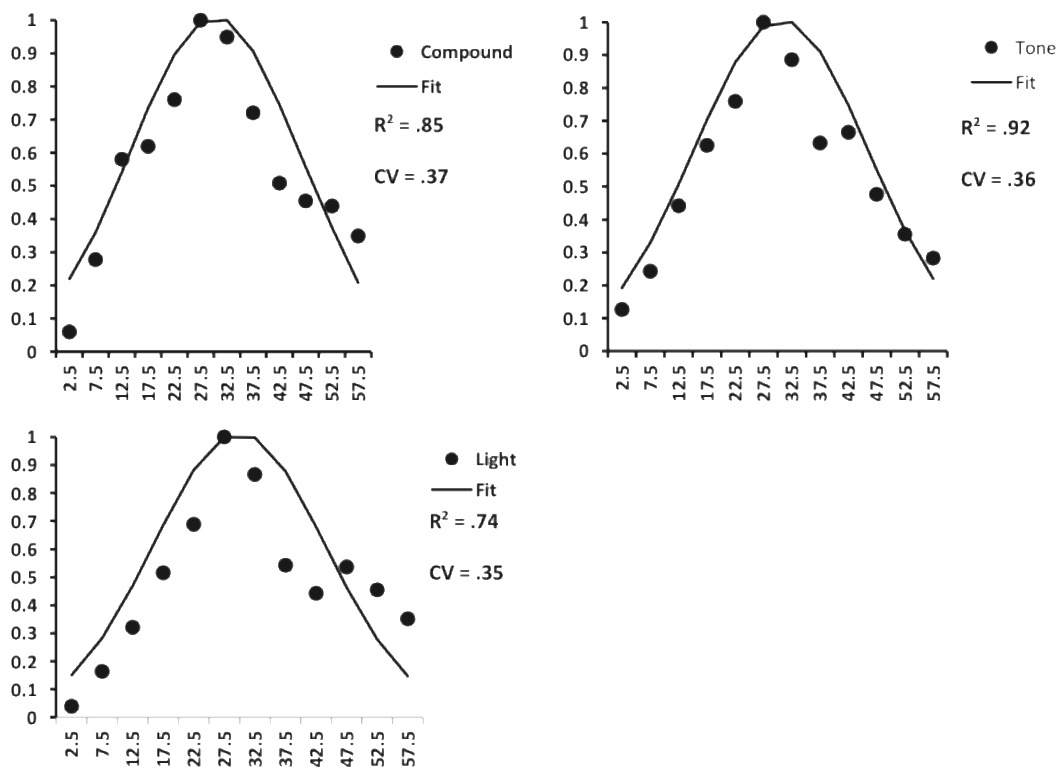
Figure 3.7. Gaussian curves fitted to compound, tone, and light data from probe trials.
CV = Coefficient of Variation.

Discussion

Experiment 1 demonstrated the successful use of the Manners Minder apparatus to study interval timing in dogs. Reponses renforced for only the first button press 30 s after the initiation of a signal learned to withhold responding during the early part of the fixed interval and to accelerate the rate of responding at the end of the interval. This pattern of responding was acquired rapidly by some dogs and required more training trials for others. Finally, dogs showed the acquisition of appropriate responding to an FI schedule when presented with either a tone + light compound or with a light stimulus alone.

A second important finding of Experiment 1 is that peak procedure timing curves like those traditionally found in other species (S. Roberts, 1981; W. Roberts et al., 1989) could be replicated with dogs. When tested with 60-s probe trials after FI 30-s training, all dogs in the compound group showed peak responding around 30 s when the compound tone + light cue was presented and when the tone alone was presented, but not when the light only was presented. Dogs trained on the FI 30-s schedule with only the light cue also showed peak responding near 30 s when tested with light probe trials.

The third important finding of Experiment 1 is that tone overshadowed light in the control of dogs' timing. A striking difference in control of responding by time interval was seen between dogs trained on the FI 30-s schedule with tone + light and dogs trained with light alone. When tested for time control with 60-s nonreinforced probe trials, dogs trained to respond to the light alone signal showed peak time curves that peaked sharply around 30 s. By contrast, dogs trained with tone + light showed relatively flat curves on light probe trials, with no indication of a peak near 30 s. As Pavlov (1927) found in his salivary conditioning experiments, presentation of an auditory stimulus in compound with a visual stimulus

appeared to eliminate accurate responding in dogs otherwise controlled by the visual stimulus. An important difference between the experiment reported here and Pavlov's finding should be pointed out. Although Pavlov showed failure of association between a light stimulus and food when the light stimulus was presented in compound with a tone, the dimension that controlled responding in the current experiment was time. Tone and light were carrier stimuli in which time duration was presented. These findings then suggest that failure to attend to the light when it was presented in compound with the tone prevented the time information it carried from being processed.

Experiment 2

Experiment 2 sought to determine how dogs would perform in a temporal bisection task (Church & Deluty, 1977). In Church and Deluty's original task, rats were taught to discriminate between light signals of 2-s and 8-s duration. Over 20 training sessions, rats learned to discriminate between these signals by pressing one lever after 2 s and another lever after 8 s. They were then tested with nonreinforced probe trials of intermediate durations. A psychophysical curve plotting the proportion of choice of the 8-s correct lever against probe durations yielded an ogive with the steepest rise in the curve between 3 and 5 s. Importantly, Church and Deluty found that the point of indifference for rats (the point at which their proportion of "long" choices was close to .50) was at the 4-s duration. This finding is of significance because 4 s is the geometric mean of the 2- and 8-s training durations (because the ratio between 2 and 4 s is equal to that between 4 and 8 s). Church and Deluty's findings suggested that rats were sensitive to the relative duration, rather than to the absolute duration of elapsed time, a finding that supports the principal of scalar invariance, as proposed by SET.

Experiment 1 demonstrated the presence of an overshadowing effect, as dogs trained with the tone + light compound stimulus showed peak responding near 30 s when tone + light and tone alone probes were tested but showed little control of responding by light-only probes. In Experiment 2, we sought to determine how dogs would perform in a temporal bisection task and whether an overshadowing effect would again be found. Dogs in the experimental group were trained to discriminate between 2- and 8-s durations of a tone + light compound and eventually were tested with compound, light-only, and tone-only probes that lasted for intermediate durations. A control group was also used, in which dogs were trained and probed with light only. This light-only control is important, as the dogs' ability to discriminate stimuli in a light-only condition eliminates the possibility that the dogs are simply unable to process the light stimulus and shows that a failure to do so in the experimental condition is most likely the result of overshadowing. Experiment 2 then complements Experiment 1 by determining whether similar timing and overshadowing effects are found with these different procedures.

Method

Subjects.

The subjects were six dogs of various breeds. One of these dogs (Cash, a rough collies) was a subject in Experiment 1.   Additional subjects included Sedona, a rough collie, Gilbert and Stella, two Parson Russell terriers, Jasper, a whippet, and Topps, a German Shepherd Dog. Three of these dogs were male (Cash, Jasper, and Gilbert), and the other three dogs were female (Sedona, Stella, and Topps). All dogs were between the ages of 2 and 5 years (mean age = 3.5 years). All dogs had received at least basic obedience training and were in good health with vaccines in good standing.

Both Stella and Gilbert were extensively trained in nosework. Given that both apparati were filled with the same amount of pellets, it is not believed that either dog was making their choices based on olfactory cues. Sedona and Cash are both owned by the author of this paper. They were therefore never handled by their owner during testing, also she did at times record their data by standing behind them, out of sight. Given that this task is not social in nature and that their owner was not in sight, it is not believed that their relationship with their owner had any influence on their performance in this task.

Apparatus.

A second Manners Minder apparatus was used in Experiment 2. The small black box used to emit light, tone, or light-tone compound stimuli was also used and placed between the two Manners Minder devices.

Procedure.

All dogs were tested in the same darkened room used in Experiment 1. The two identical Manners Minder apparati were placed 2 m apart. The small black box emitting the light and tone stimuli was placed between the two Manners Minders. Experimenter 1 held the dog directly in front of the light box, 1.5 m in front of the apparatus. Markers on the floor indicated where each piece of the apparatus and the dog should be placed for testing. Experimenter 1 was also responsible for changing the settings on the black box between trials (varying the settings between light and/or tone, and setting the duration of the signal). Experimenter 2 sat at the back of the room, manually recording data, and instructing Experimenter 1 as to which settings were required for the upcoming trial. The intertrial interval was approximately 60 s. Once the settings were adjusted on the apparatus, the dog was held in place to watch the light and/or hear the tone for the duration of the signal.

Caution was taken to ensure that the dog sat very straight, so that it was not leaning towards one feeder or the other. If possible, the dog sat without the experimenter holding onto its lead or collar. If the dog needed to be held in place, care was taken to make sure that the dog was held from behind on a very loose lead, to ensure that the experimenter could not "steer" the dog in either direction. Both Experimenter 1 and Experimenter 2 were placed behind and therefore out of sight of the dog, in order to prevent any type of gaze-related or Clever Hans cues.

Dogs were initially trained simply to discriminate between 2-s and 8-s signals, by choosing the appropriate feeder. Four dogs (Gilbert, Jasper, Cash, and Sedona) were trained with the tone + light compound signal in the experimental group, and two dogs (Stella and Topps) were trained with the light signal in the control group. The assignment of subjects was counterbalanced such that for three dogs, the machine on the right was the correct choice for a 2-s trial and the machine on the left was the correct choice for an 8-s trial, and this assignment was reversed for the remaining dogs. In this experiment, the dogs did not have to hit the square white button in order to indicate a response. They simply had to approach and be within 30 cm of the correct machine (as indicated by a mark on the floor). This was done to prevent the dogs from becoming bored or frustrated with the task. If the dogs chose the correct machine on a trial, their response was reinforced by the selected machine. If the dogs chose the incorrect side, they were simply told "too bad" in a neutral tone, and the trial was concluded.

In order to help dogs acquire this discrimination learning, the black box that emitted light and/or tone stimuli was initially moved so that it was closer to the location of the correct feeder. This procedure provided an extra spatial cue, which helped the dogs to learn what

was expected of them. This spatial cue was eventually faded out, until the black box was placed directly between the two Manners Minders. Once a dog solved the discrimination task (by reaching a criterion of 75% within a session without any spatial cue), the dog began to receive probe trials. Probe trials included values of 2, 3, 4, 5, 6, 7, and 8 s. Dogs received one probe at each duration in every session, and the probes were randomly distributed among the dogs' usual 2- and 8-s training trials (they received eight of each of these trials per session, for a total of 23 trials per session once probes were included). For all probe trials, the dogs were reinforced regardless of which side they went to—this is a departure from the procedure of previous studies, where animals given such probe trials are typically not reinforced. The decision to reinforce responses made by the dogs on these probe trials was made due to the fact that for some of the subjects, responding extinguished very quickly if reinforcement was not provided. For dogs in the experimental group, probes initially consisted of the tone + light compound, but were eventually dissociated such that in a given session, the dog received all light-only or all tone-only probes. Dogs in the control condition received the light-only probes. All dogs were tested 2-5 days per week, depending upon their availability. Dogs in the experimental condition received light-only and tone-only probes on alternating days. Testing sessions lasted approximately 40 min.

Results

The dogs varied in the number of trials taken to reach the 75% accuracy criterion before probe trial testing. The four dogs trained with the tone + light cues, Jasper, Gilbert, Sedona, and Cash, required 220, 280, 140, and 120 trials, respectively. The two dogs trained with the light cue alone, Topps and Stella, required 200 and 280 trials, respectively.

Psychophysical curves were plotted for each dog by calculating the proportion of test trials at each stimulus duration on which it chose the long (8 s) duration response. Figure 3.8 shows these psychophysical curves for stimulus durations lasting from 2-8 s Curves are shown for each of the four dogs trained with the compound tone + light stimulus and subsequently tested with compound, tone, and light probes. Each dog shows a sharply rising curve for tone probe trials. In fact, the tone curves show somewhat better control of choice than the compound stimulus curves. Three of the dogs, Gilbert, Cash, and Sedona, all show lower choice of the long alternative at short (2-4 s) durations of the tone probe than of the compound probe. Sedona also shows clearly higher choice of the long alternative at long durations (6-8 s) of tone than of the compound. Jasper shows equivalent control of choice by both the tone and the compound stimulus. These data also show that the durations of the light probes exerted little control over choice of the long alternative. Jasper shows a flat curve of around 0.5 proportion of choices of the long alternative. Gilbert and Cash show curves that begin at a relatively high level of choice of the long alternative (0.4 to 0.5) and then rise and flatten out at higher levels. Sedona shows a sawtooth curve, indicating little sensitivity to light duration. The mean curves for all four dogs clearly show that dogs' choices were controlled by durations of the tone and compound stimuli but not by durations of the light stimulus.

An ANOVA was performed on the data in Figure 3.8 containing the three probe cues as one factor and the seven probe durations as the other factor. This analysis yielded significant effects of probe duration, $F(6, 18) = 39.49$, $p < .01$, $\eta_p^2 = .93$, and of the probe stimulus x probe duration interaction, $F(12, 36) = 8.71$. $p < .01$, $\eta_p^2 = .74$. This analysis
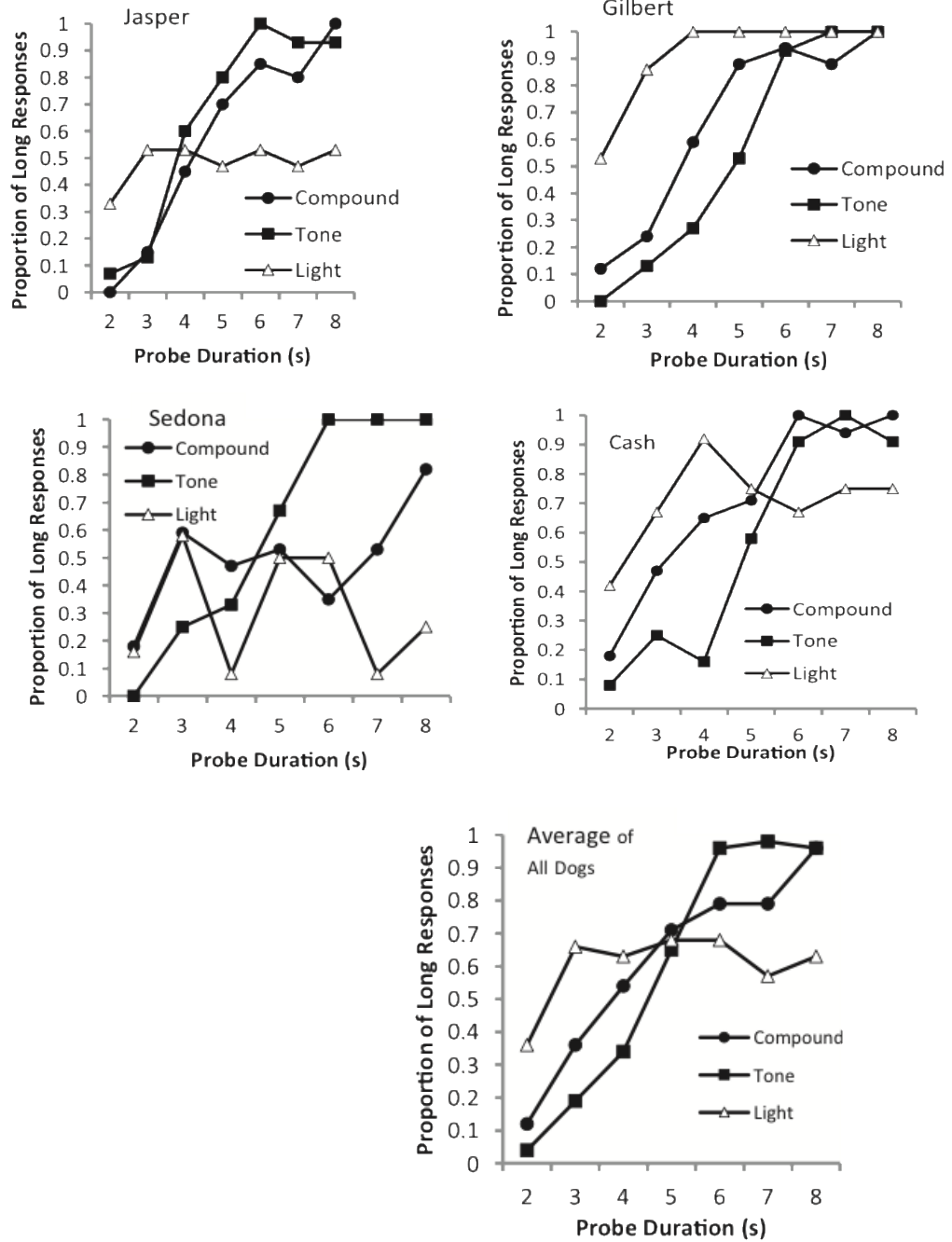
Figure 3.8. Proportion of long responses at probe durations from 2-8 s for tests with tone + light (compound), tone alone, and light alone.

supports the impression seen for individual dogs that they kept track of the duration of the tone component but not the light component of the compound stimulus.

Given the orderly psychophysical curves obtained with the compound and tone stimuli, we computed for each curve the point of subjective equality (PSE). Linear regressions of the proportion of long responses were computed for successive groups of three points along each curve. The regression equation with the highest slope was then used to obtain the PSE as the point where 50% long responses were made (Church & Deluty, 1977; Santi, Keough, Gagne, & Van Rooyen, 2007). When tested with the compound tone + light stimulus, the four dogs Jasper, Gilbert, Cash, and Sedona had PSEs of 4.27, 3.81, 3.36, and 6.64 s, respectively. When tested with the tone stimulus alone, the PSEs were 4.1, 4.7, 4.91, and 4.51 s, respectively. The mean PSEs were 4.52 s for the compound and 4.56 s for the tone and did not differ significantly, $t(3) = .04$. Thus, dogs showed average PSEs midway between the geometric mean (4 s) and the arithmetic mean (5 s) of 2 and 8 s.

Additional standard measures of sensitivity were computed from the psychophysical curves. The difference limen (DL) was calculated as the difference between the 75% long and 25% long responses, and the Weber fraction (WF) was calculated by dividing the DL by the PSE. For Jasper, Gilbert, Cash, and Sedona, the DLs for the compound stimulus were 1.82, 1.56, 2.12, and 2.12 s, respectively. The DLs for testing with the tone stimulus were 1.49, .75, .66, and .74 s, respectively. The mean DL for the tone stimulus (.91 s) was significantly lower than the mean DL for the compound stimulus (1.9 s), $t(3) = 3.76$, $p = .03$. Each dog's WF was lower when tested with the tone than when tested with the compound. When tested with the compound stimulus, the WF for Jasper, Gilbert, Cash, and Sedona was .43, .41, .63, and .32, respectively. When tested with the tone alone, the WFs were .36, .16,

.13, and .16, respectively. The mean WF for tone was .20 and that for the compound was .45, and the difference between these means approached statistical significance at the .05 level, $t(3) = 2.65$, $p = .08$. In general, these findings suggest that dogs were more sensitive to changes in time duration when presented with the tone alone than when presented with tone + light.

Figure 3.9 shows the psychophysical curves for the control dogs trained and tested with only the light stimulus. Both Topps and Stella show rising curves, indicating control of choice by duration of the light stimulus. The panel showing the average curve for both dogs includes the light probe curve obtained from dogs trained with the compound stimulus. With the exception of the 2-s duration, the compound group shows a flat curve for durations 3-8 s, whereas the control dogs show a steadily rising curve from 2-8 s. A group x probe duration ANOVA performed on these data revealed a significant effect of probe duration, $F(6, 24) = 5.55$. $p < .01$, $\eta_p^2 = .72$, and a group x probe duration interaction that approached significance at the .05 level, $F(6, 24) = 2.18$, $p = .08$, $\eta_p^2 = .28$.

Parameters of the psychophysical curves shown in Figure 3.9 were calculated for each dog. The PSEs for Topps and Stella were 4.12 and 4.37 s, respectively. The DLs were 3.48 and 2.86 s, respectively, and the WFs were .84 and .65, respectively. In general, Topp's and Stella's sensitivity to time duration on light probe trials was not as great as that of the dogs tested with tone probes in the compound group but was greater than that of the same dogs in the compound group when tested with light.
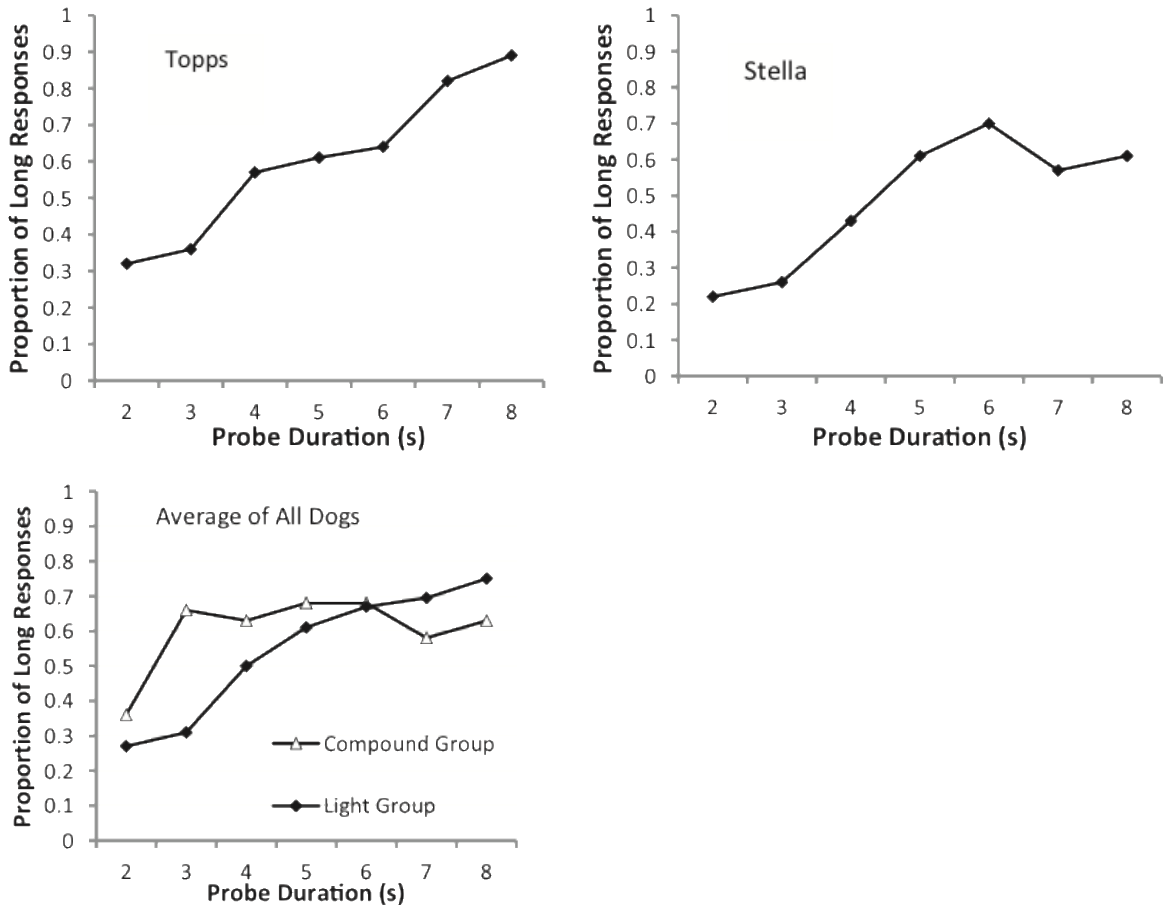
Figure 7. Psychophysical curves for control dogs tested with light only. The average panel show*s* performance with the light probe in the compound group for comparison.

Discussion

The findings of Experiment 2 nicely complement those of Experiment 1. Dogs learned to discriminate between 2- and 8-s durations of compound tone + light stimuli. Separate tests with tone and light probe cues of intermediate duration revealed that dogs were using duration of the tone cue and not the light cue to make the temporal discrimination. As in Experiment 1, it appears that the tone cue overshadowed the light cue. Training and testing with control dogs presented with only the light cue showed that these dogs learned the temporal discrimination and showed sensitivity to light duration when probed with lights of intermediate durations. Both experiments suggest that dogs discriminated light durations when the light cue was presented alone but became insensitive to light duration when the light was presented in compound with a tone.

General Discussion

The preceding experiments demonstrate that dogs are sensitive to time and can estimate the duration of a fixed time interval. This ability was shown using two different procedures previously used in a number of experiments to show interval timing in other species, most commonly rats and pigeons. In Experiment 1, dogs were trained to respond for reinforcers delivered from a Manners Minder using an FI 30-s schedule; the first response made 30 s after the onset of a signal was reinforced. Over repeated training trials, dogs developed response curves showing less responding in the early part of the FI schedule and increased responding as 30 s approached. They were then tested with nonreinforced probe trials that lasted for 60 s. Clear evidence of interval timing was shown by response curves that peaked near 30 s. In Experiment 2, a temporal bi-section task was used in which dogs learned to make different responses after experiencing a 2-s or an 8-s duration cue. When

dogs were tested at durations intermediate between 2 and 8 s, they produced rising psychophysical curves of long choices indicating clear sensitivity to time duration. The dogs' point of indifference or PSE, the point at which they judged a duration as midway between the short and long training durations, occurred at durations midway between 4 s and 5 s.

Although dogs clearly showed the ability to judge time duration accurately, a caveat to this claim is the finding that that their ability to judge time duration depended on the cue used to present time duration and the context in which that cue was presented. Dogs were able to time a fixed interval and to discriminate between shorter and longer intervals using both light and tone. A significant overshadowing effect was present, however, such that when dogs were initially trained with tone + light, tone took precedence, leaving the dog unable to utilize light alone as a cue for time duration.

The findings reported here are similar in some ways to those found by Pavlov with dogs nearly a century ago (Pavlov, 1927). Pavlov also found evidence that dogs could track intervals of time. In his delay conditioning experiments, it was found that dogs timed the interval between the initiation of the CS and the delivery or the food US. Timing was shown by the fact that dogs only began to show significant amounts of salivation near the time when the US was scheduled to appear. The findings of Experiment 1 may be seen as an operant analog of the Pavlovian delay conditioning procedure. However, our experiments used operant techniques for studying timing developed relatively recently (Church & Deluty, 1977; S. Roberts, 1981). As in the Pavlovian procedure, dogs withheld the maximum number of operant button presses until near the end of the 30-s FI, and the decline in responding after 30 s, shown on 60-s probe trials, indicated the precision of dogs' timing.

The finding of overshadowing in these experiments also reflects Pavlov's (1927) finding of overshadowing in his experiments. Dogs conditioned to make a salivary response to a compound of a tone from a tuning fork and a series of lamps subsequently elicited salivation when played the tone but not when shown the lamps. In both Experiments 1 and 2, dogs trained to discriminate time intervals from the onset of a compound tone + light stimulus subsequently showed acute sensitivity to time duration when tested with the tone but not with the light. Importantly, it was shown that the presence of the tone overshadowed or prevented the light from being used as a discriminative stimulus. Control dogs trained with light alone showed control of responding by light in both experiments. Beyond the difference between Pavlovian and operant procedures, another important difference should be pointed out. In Pavlov's overshadowing experiment, dogs were trained to respond to tone + light as a cue signaling the delivery of food. In the current experiments, the discriminative stimulus for food delivery upon the execution of an operant response was time duration. The tone and light cues were then carriers of the more abstract time duration cue. Nevertheless, these experiments show that the presence of light during the presence of tone prevents dogs from attending to the light and thus prevents them from using the light's duration as a cue for accurate responding.

Dogs' sensitivity to the tone and light cues used in these experiments should be considered. Dogs are known to have excellent hearing over ranges from 50-100 Hz to 50,000-60,000 Hz (Coren, 2004). Moreover, dogs' thresholds between 1,000 to 8,000 Hz were found to be 10-20 dB lower than those of humans (Lipman & Grassi, 1942). Canine visual acuity, however, is inferior to that of humans. The canine retina contains approximately 115,000 retinal ganglion cells (Peichl, 1992), whereas the human retina

contains up to five million ganglion cells (Watson, 2014). Unlike the human retina, which has a fovea where retinal ganglion cells are concentrated at one point, dogs have retinal ganglion cells arranged in a visual streak across the retina. The canine eye consists primarily of rods, making dogs adept at seeing in low lighting conditions, and sensitivity is increased by an additional structure called the *tapetum lucidum* that reflects light passing through the retina back to it (Miller & Murphy, 1995). In the experiments reported here, the tone stimulus was a 2800-Hz tone presented at an intensity of 78 dB, and the light stimulus was a 4-W bulb presented in darkness. Thus, both stimuli were well within the dogs' auditory and visual ranges of sensitivity.

It could be argued that different results would have been found with different intensities of noise or light. Mackintosh (1976) examined overshadowing in rats using light and noise stimuli to condition a fear response produced by shock. Bar press suppression scores showed that intense noise overshadowed moderate light intensity and that intense light intensity overshadowed moderate noise intensity. Further, at moderate levels of noise and light, reciprocal overshadowing was found. Thus, it is possible that dogs would have shown less overshadowing with a brighter light or a weaker tone. It was our impression that the light and tone intensities used in Experiments 1 and 2 were of moderate level. Yet, we found no evidence of reciprocal overshadowing. That is, curves obtained with tone probe stimuli revealed clear sensitivity to time and were similar to the tone + light curves found in both experiments, indicating that the light stimulus did not overshadow the tone stimulus.

Another consideration in understanding these results may be a dog's sensitivity to being tested in a darkened room—is there any reason that this should have an effect on a dog's behaviour? In one study using a visual perspective-taking task (Kaminski, Ditsch &

Tomasello, 2013), it was found that dogs were more likely to steal a piece of food forbidden to them by their owner when they in a darkened room, than if they were in an illuminated room. The purpose of this study was very different from our own, as it raises the possibility that the dogs were able take into account the human's visual access to the food while making their decision to steal it. With respect to the current study, however, it is worth noting that the dogs appeared to be sensitive to the nature of the lighting in the room, and adjusted their behaviour accordingly.

At the time of this writing, we could find no published articles on the topic of interval timing in dogs. One alternate hypothesis accounting for timing in dogs, however, is the idea that dogs may be "smelling" time (Horowitz, 2016). It is hypothesized that dogs are attuned to the intensity of scent in the air. For example, if an owner leaves her home everyday at 9 am, her scent will be at its strongest just after she leaves. Throughout the day, the owner's scent will dissipate. Therefore, if the owner returns everyday at 5 pm, the dog may come to anticipate the owner's return based upon the amount of scent remaining in the air. While it is possible that dogs may be able to track time via olfaction, this interesting hypothesis remains untested and would seem to be a mechanism by which a dog would detect time of day.   The interval timing found here with dogs and in a number of other species may be best explained in a manner consistent with SET theory or other alternative theories about timing short durations.

Overall, the dogs demonstrated a thorough understanding of the timing task, and demonstrated peak time curves consistent with those seen in other species. There were, however, some differences between subjects in their respective timing curves. This was true for the peak time curves in Experiment 1, as well as in the data for the light-only probes in

Experiment 2. With the peak time curves, some dogs demonstrated a "cleaner" curve, with button pressing maximized around 30 s and immediately dropped off, while other dogs maintained a higher rate of responding after 30 s. Thus, Kip in the compound stimulus group and Ruby in the light-only group showed symmetrical curves, but Harriet and Cash in the compound group and Pepper and Lucy in the light-only group showed higher responding after 30 s than before 30 s. This behavior has been demonstrated previously in pigeons (Kirkpatrick-Steger, Betti, & Wasserman, 1996) and was explained as the animal anticipating the approach of the next fixed interval. In the temporal bi-section task, timing behavior was seen for animals in the experimental group when they were given the tone + light compound, as well as when they were given the tone-only probes. In these conditions, animals consistently discriminated between 2 s and 8 s and demonstrated psychophysical curves showing time discrimination. When given light-only probes, however, all dogs in the compound stimulus group not only failed to properly discriminate the light signals but seemed to use different approaches in response to the probes. Gilbert and Cash tended to choose the long stimulus alternative on most trials when confronted with the light probe. This behavior suggests that they simply gave up attempting to solve the problem when confronted with the light cue. Jasper and Sedona, on the other hand, showed a mixture of short and long responses across probe durations. These dogs then may have been attempting to utilize the light cue, as they switched sides consistently between trials.

Dogs' CVs for fitted peak time curves were closely similar (.35-.37) for probe tests with a tone, light, and tone-light compound in Experiment 1 (Figure 3.7). In terms of the comparative analysis of interval timing reported by Lejeune and Wearden (1991), these CVs suggest that dogs' sensitivity to intervals of time is about the same as that of pigeons and

possums (Sargisson et al., 2016), lower than that of cats, rats, monkeys and humans, but higher than that of fish and turtles. Given the higher CVs found with dogs in the current study, it might be argued that domestication has caused some loss of sensitivity to time in dogs (Frank, 1980). In this regard, studies of interval timing in wolves, from which dogs descended, would be of interest. As pointed out by Bitterman (1965), however, such comparisons across species of absolute values from behavioral experiments may be problematic. Changes in contextual variables such as the stimuli, the type of response made, or the reinforcer used might yield higher or lower CVs.

Like many animals, dogs have been shown to be highly sensitive to the motion of visual stimuli (Miller & Murphy, 1995). An interesting extension of the current experiments might be to determine if an overshadowing effect appears when a moving or flashing light cue, rather than a stationary light cue, is used. Might a dog time the duration of a moving visual cue accurately, even in the presence of a tone stimulus? Understanding the salience of these cues for dogs could have important implications for their training. For example, if visual cues combined with auditory cues are not that useful in dog training, then it makes sense that auditory commands, rather than hand signals, should be emphasized. This information could be particularly important in the training of various types of service dogs because hundreds of hours are put into the training of guide dogs and police and military dogs. Understanding which cue properties have the greatest salience to dogs may have implications for training them in the most efficient and economical manner.

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Chapter 4

Spatial Memory in Domestic Dogs: New Approaches and Individual Differences?

Krista Macpherson and William A. Roberts

Abstract

Although several studies have examined spatial ability in dogs, most of these studies have focused on spatial understanding and navigation, rather than spatial memory capacity. In an earlier study, Macpherson and Roberts (2010) attempted to examine spatial memory using an apparatus commonly used to study these processes in rats, the 8-arm radial maze. These studies demonstrated spatial memory ability in domestic dogs, as well as preference for the use of a win/shift strategy. Performance of the dogs, however, was surprisingly low compared to that of rats and pigeons on analogous tasks. Given that the radial maze was designed to mimic the subterranean environment of the rat, an argument could be made that the radial maze is simply not the most appropriate apparatus for testing domestic dogs. Rather than having dogs search for food in the eight arms of the maze, the present studies had them search for food within the four corners of a large area (an empty classroom in Experiment 1, and an outdoor field in Experiment 2). Food items were hidden under plastic flower pots, which the dogs had previously been trained to knock over. Additionally, these studies examined the potential interaction between reference and working memory, by comparing the dogs' performance in locating rewards hidden consistently in the same location during the test phase (reference memory), versus rewards hidden in a different randomly-selected location from trial to trial (working memory). Dogs' performance varied across subjects, and implications of these individual differences are discussed.

Keywords: spatial memory, reference memory, working memory, dogs

Spatial Memory in Domestic Dogs: New Approaches and Individual Differences

Locating and remembering the location of food, water, mates, and predators is essential to the survival and reproduction of animals in their natural habitats. Extensive studies of spatial cognition have shown that animals use a number of cues and mechanisms to navigate their environments (Healy, 1998; Roberts, 2001; Shettleworth, 1998). These include both intrinsic cues provided by an animal's own movements, as well as extrinsic cues emanating from the animal's environment. Intrinsic cues include the ability of numerous insects and vertebrates to take a direct path home after taking a tortuous route to some distant point (path integration). Extrinsic environmental cues, on the other hand, allow animals to navigate through spatial environments by using geometric relationships between objects (Cheng, 1986), landmarks and beacons (Collett & Zeil, 1998), and by the computation of distance and direction vectors using multiple landmarks (Menzel, Geiger, Joerges, Müller, & Chittka, 1998).

In addition to the study of mechanisms involved in navigation, a number of studies have indicated that many animals have considerable spatial memory ability, both in terms of the number of locations that can be stored and in terms of the length of time over which locations in space can be remembered. These abilities are particularly impressive in food-caching species of birds; Clark's nutcrackers bury as many as 33,000 seeds in the fall and recover them throughout the winter (Tomback, 1980), and Black-capped chickadees accurately recover seeds cached in trees in a laboratory at retention intervals as long as 28 days (Hitchcock & Sherry, 1990). Rats have also been shown to be highly accurate in keeping track of locations on a 17-arm maze (Olton, Collison, & Werz, 1977) and on a hierarchical maze that involved 24 different locations (Roberts, 1979).

The ability to remember spatial locations has also been demonstrated in nonhuman primates. Menzel (1973) reported that when shown the location of 18 different food items in an open field, chimpanzees accurately retrieved all of the food items and did so by traveling the shortest distance possible between food locations. In a series of experiments using a task somewhat analogous to the radial maze, MacDonald and her colleagues had animals search for food in eight different containers placed at different positions in an enclosure. An ability to visit all of the food locations with a very low incidence of revisits was found in yellow-nosed monkeys (MacDonald & Wilkie, 1990), an Old-World species, in marmoset monkeys (MacDonald, Pang, & Gibeault, 1994), a New-World species, and in two species of apes, gorillas (MacDonald, 1994) and orangutans (MacDonald & Agnes, 1999). In follow-up studies using a win-stay/win-shift procedure, these species visited the containers and found that only four of them at random contained food. In a subsequent test phase, they returned to the enclosure and could visit any of the containers, but only the previously baited four containers were baited (win-stay condition) or only the four previously empty containers were baited (win-shift task). In general, all of these species were above chance in their accuracy on these tasks.

The Study of Spatial Capacity in Dogs

Though widespread interest in canine cognition is relatively recent in the history of comparative psychology, several studies have investigated spatial understanding and navigation in dogs. Initial studies with dogs, for example, concluded that they were capable of solving an invisible displacement task (Gagnon & Doré, 1992, 1993, 1994). In the traditional version of this object permanence task, an item is placed in an opaque container or "displacement device", within view of the subject. The displacement device is then placed

behind an occluding screen, and the object is removed and left behind the screen, without the subject seeing that the item was removed. The displacement device is then removed from behind the screed and tipped on its side, allowing the subject to see that it is empty. In order to solve the task, the subject must presumably recognize that the object of interest must be located behind the screen. Later findings, however, suggested that dogs may not understand invisible displacement. Collier-Baker, Davis, and Suddendorf (2004) and Fiset and LeBlanc (2007) found that in a version of the task using multiple screens, dogs tended to choose a box adjacent to the position of the displacement box. Thus, when the displacement device was left near the correct target box, dogs performed accurately, but, when it was left near an incorrect box, their performance dropped below chance.

In studies of spatial navigation in dogs, the role of both egocentric and allocentric cues has been studied in dogs' ability to find hidden rewards. Cattet and Etienne (2004) showed dogs the location of food and then led them to the opposite side of an enclosure while blindfolded and wearing earphones. When released, dogs went directly to a location near the hidden food, indicating use of path integration. Fiset (2007) trained dogs to find a buried object placed at a constant distance and direction from two landmarks. On tests when the landmarks were shifted laterally, vertically, or diagonally, dogs searched at locations that were partially but not completely shifted as far as the landmarks, suggesting that dogs had encoded the target location by using both the landmarks and global cues provided by the testing room. Based on this evidence, Fiset, Landry, and Ouellette (2006) suggest that dogs use both egocentric and allocentric cues in a hierarchical fashion. When dogs can take a linear path between their spatial position and a hidden target location, they maintain a vector containing distance and direction information to the target over a time interval in which a

barrier is placed between them and the target. When dogs search for a hidden object that has disappeared or been visibly displaced, their preferred strategy is to use egocentric cues to find it, such as a linear path or dead reckoning. If these cues are unavailable, however, dogs use allocentric cues, such as the position of a target relative to landmarks and global cues (Fiset, Gagnon, & Beaulieu, 2000; Fiset, Beaulieu, LeBlanc, & Dube, 2007).

Although considerable research has been carried out to investigate spatial displacement and navigation in dogs, little work has been performed to examine dogs' spatial capacity or ability to remember a number of different spatial locations. A number of experiments have shown that dogs attend to human cueing and perform better in tasks when cued by a person. For example, both adult dogs and puppies use human head pointing, head turning and gaze as cues to the hidden location of food (Agnetta, Hare, & Tomasello, 2000; Hare & Tomasello, 2005; Miklósi, Polgardi, Topál, & Csanyí, 1998; Miklósi, Pongrácz, Lakatos, Topál, & Csanyí, 2005; Udell, Giglio, & Wynne, 2008). Dogs' sensitivity to human cueing has been thought to be the result of the fact that they have lived in close association with humans for at least 10, 000 years (Pollinger et al., 2010). Through artificial selection by humans, dogs have come to possess traits highly adapted to life among humans, including communicative, social, cooperative and attachment behaviors (Miklósi & Topál, 2005; Miklósi, Topál, & Csanyí, 2004). Overall, dogs have been shown to be more skillful than a vast number of other species in tasks requiring them to respond to human communicative gestures (Reid, 2009). If dogs have been selected for human-like abilities, it could be argued that they should demonstrate sophisticated spatial memory ability, as seen in studies with humans and non-human primates.

An alternate possibility is that dogs have paid an adaptational price for their role in human society. Frank and Frank (1982) argued that domestication of dogs had actually selected against cognitive processes that may be present in the wolf. In a comparative study of six-week-old wolves and dogs, they found that wolves outperformed dogs in a problem solving experiment that required animals to find their way past barriers of varying length. Bräuer, Kaminski, Riedel, Call, and Tomasello (2006) hypothesized that dogs should be especially skillful at employing human social cues, while apes should be skillful at using physical cues provided by objects to be discriminated. It was found that dogs readily used human pointing, while chimpanzees did not. By contrast, apes discriminated between containers well when the containers provided differential auditory cues, but dogs did poorly based on these physical properties. In a string-pulling task, dogs failed to be able to infer the path of a baited string when strings were crossed (Osthaus, Lea, & Slater, 2005), but chimps (Köhler, 1925) and ravens (Heinrich & Bugnyar, 2005) readily solved such problems. These studies suggest the possibility that the spatial memory capacity of dogs might be reduced relative to species that did not undergo intense human domestication.

The Study of Spatial Memory in Dogs Using the Radial Maze

In an earlier effort to study spatial memory in the domestic dog (Macpherson & Roberts 2010), a large radial maze was constructed for use with domestic dogs. The radial maze has been used to study spatial memory in rats (Olton & Samuelson, 1976), gerbils (Wilkie & Slobin, 1983), pigeons (Roberts & Van Veldhuizen, 1985), fish (Roitblat, Tham, & Golub, 1982), and other species, but at that time no studies of dogs had been carried out with this apparatus. A large, enclosed 8-arm radial maze was therefore constructed, and accommodated dogs of different sizes. Dogs were given repeated trials on the maze, and a

record of their arm entries was kept for analysis. The initial experiment examined dogs'

working memory on the maze when all arms were baited and a dog could choose freely

among all the arms. Dogs in this experiment learned to enter all eight arms with

progressively fewer arm visits over trials. The second experiment studied dogs' working

memory for arm locations when they had to remember a subset of four random arm locations

initially visited. In addition, the second experiment examined whether dogs showed better

retention when required to use a win-shift or a win-stay strategy to enter baited arms. Like

many other species, dogs performed better with the win-shift rule than with the win-stay rule.

In a third experiment, reference memory was investigated by using a 4-arm maze on which 0,

1, 3 and 6 pieces of food were consistently placed on different arms. Dogs learned to visit

the arms with the larger amounts before the arms with the smaller amounts. These

experiments allowed for comparisons to be made between dogs' spatial memory and those of

other species. Dogs' memory capacity in these studies was found to be surprisingly low,

compared to rats and pigeons tested on an analogous task (Beatty & Shavalia, 1980; Roberts

& Van Veldhuizen, 1985).

In another study using a radial maze (Craig, Rand, Mesch, Shyan-Norwalt, Morton &

Flickinger, 2012), serial position was examined. According to the serial position effect,

performance on a recall task is best for items at the beginning of a list (the primacy effect)

and at the end of the list (the recency effect). Primacy and recency effects have been

demonstrated in domestic dogs. Both old and young dogs (Tapp et al., 2003) have shown

significant primacy and recency effects in a delayed non-matching to position task. Craig et

al. tested serial order on the radial maze by first having dogs visit seven of the eight arms,

one at a time. Once these seven forced choices were completed, dogs were given a choice

between a previously visited (distractor) arm, and the remaining unvisited (correct arm).

Dogs chose the correct arm in 83.8% of trials. Furthermore, dogs chose the correct arm more often when the distractor arm was in the first serial position of the initial seven forced choice arms, suggesting a primacy effect.

Ecological Validity of the Radial Maze with Dogs?

The radial maze was originally created by David Olton (Olton & Samuelson, 1976) to mimic the natural subterranean environment of wild rats--a central chamber below ground, with multiple tunnels extending from that central hub. This is not at all how a dog lives, and so the results of the Macpherson and Roberts (2010) studies may be an indication that the radial maze is simply not be the best apparatus for testing spatial memory in the domestic dog. It should be noted, however, that in the Craig et al. (2012) studies, which used a radial maze similar in dimensions and construction to the one used by Macpherson and Roberts (2010), superior spatial memory performance was found in dogs in several tasks (though the performance of dogs in this task was still not on par with what is typically seen in rats). These differences in findings may be the result of subtle differences in environmental or extramaze cues surrounding the respective mazes. For example, whereas the maze in the Macpherson and Roberts (2010) studies was often moved between daily sessions (due to logistical issues), the Craig et al. (2012) maze remained in one location, which may have provided more consistent cues to be utilized by the subjects. Thus, further research will be needed to completely assess dogs' spatial memory abilities, as well as the effectiveness of the radial maze as an apparatus in the study of canine spatial memory.

Competition between Working and Reference Memory Systems

The question of whether or not multiple memory systems exist has been the topic of considerable discussion in studies of both human and animal cognition. Based on early studies of short-term memory in humans, it has been suggested that working memory is a temporary storage system in which processing of information is carried out for subsequent long-term storage (Atkinson & Shiffrin, 1968). Baddeley (1992) later expanded on this model by proposing that the working memory system consists of a central executive that integrates information from subordinate systems, that include a visuospatial sketchpad (which processes information in visual or spatial form and is used for navigation) and a phonological loop (which processes information from sound). Theories of human long-term memory, on the other hand, suggest that it consists of two major components, declarative and non-declarative memory (Squire, 2004). Declarative memory is memory for factual information and events, and can be further sub-divided into semantic (memory for general information) and episodic (memory for autobiographical events) memory (Tulving, 1985). Non-declarative memory is procedural in nature, and allows us to acquire and remember fine motor skills.

Research involving physiological structures of the brain has also provided evidence that different neural systems may underlie reference and working memory. Hippocampal lesions (Olton & Papas, 1979) have been found to considerably reduce the accuracy of working memory, yet to have no effect on reference memory. In other studies (Packard et al., 1989; Packard & White, 1990), groups of rats received lesions to either the hippocampus or the caudate nucleus. Hippocampal lesions produced a large increase in working memory errors but had no effect on reference memory in a task involving using a light cue to seek a

reward. The opposite results were found for rats with caudate lesions, as these subjects experienced a significant increase in reference memory errors. Impaired working memory on a delayed matching-to-sample task (Diekamp et al., 2002a) has also been found in pigeons with lesions to the neostriatum caudilaterale (NCL).

A more recent question with regards to memory systems is how WM and RM may interact in the control of behavior when their contents are in disagreement. For example, a phenomenon familiar to most people is the loss of a recently formed WM and its replacement with memory for a well learned RM. Consider, for example, searching for your car keys. You may have a location where you generally keep your keys (on the mantle, for example). The memory for this location is a well learned habit or RM. If in a rush you leave your keys in a different location, on the table for example, your recollection of that new location is stored in WM. This scenario is an example of interaction between memory systems. If you were to search for your keys immediately, you would remember the new location on the table. If you aren't leaving the house until the next day, however, the WM will have been lost and you will likely return to the mantle to search for your keys in their typical location.

Jacoby (1991) posited that implicit (unconscious) memory may be contaminated by explicit (conscious) memory. To test this, Jacoby developed the *process dissociation procedure* (PDP), in order to compare performance under a condition in which habit (implicit memory) and recollection (explicit memory) work together resulting in retention (a "congruent" condition), versus performance under which habit and recollection are opposed to each other (an "incongruent" condition). Using performance scores from each of these conditions, measures of each type of memory were acquired under varying test conditions. Hay and Jacoby (1996) subsequently applied the PDP analysis to people's memory for word

pairs that had been previously established as strong or weak habits (RM) and then more recently presented on a single occasion (WM). Results from the PDP scores suggested that the memory systems under study were independent of one another. That is, manipulations designed to affect strength of RM affected only RM PDP scores and not WM scores, and manipulations designed to affect WM affected only WM PDP scores and not RM scores.

Tu and Hampton (2013) extended the PDP procedure to the study of memory in rhesus monkeys. Using a delayed matching-to-sample procedure to test WM, monkeys were shown a clip-art sample stimulus on a screen. Four images were then shown after a delay, with only one image matching the sample image. Habit/RM was manipulated by presenting one set of images more often than others. Thus, on different tests, the correct image that matched the sample corresponded to a relatively strong habit image (congruent condition) or corresponded to a relatively weak habit image (incongruent condition). Interestingly, when the delay or retention interval was increased, WM one-trial memory PDP scores dropped but RM habit PDP scores were unaffected—these results are strikingly similar to those found in the human PDP studies. When the probability of a sample-match pair was varied between 25% and 100% within sets of four images, RM PDP scores increased but WM PDP scores remained unchanged.

Guitar & Roberts (2015) examined the possibility that evidence could be found of independent but competing memory systems in rats, using an 8-arm radial maze. In an initial experiment, rats were trained using a win-shift procedure. In each trial, rats were given a study phase in which they were forced to enter four arms, with a food reward at the end of each arm (the other four arms were blocked off and inaccessible to the rat). After a delay, rats returned to the maze for a test phase, in which all eight arms were now available to the

rats. Importantly, for each rat, two arms were designated as reference memory (RM) arms—these arms were never baited in the study phase and always baited in the test phase. Two other arms were designated as working memory (WM) arms—among the six arms that were not designated as RM arms, whichever two arms that were not baited in the study phase on a given trial became the WM arms. RM arms were therefore in the same location every trial, while WM arms shifted from trial to trial. Under these conditions, rats showed acquisition of equivalent preference for entering the working and reference memory arms in their first four choices during the test phase.

In a follow-up study, Guitar & Roberts (2015) compared performance of rats at retention intervals of 5-s, 1-h, and 24-h, when RM and WM were congruent and incongruent. In a congruent trial, the RM arms were inaccessible during the study phase, and baited during the test phase. This arrangement made the trial congruent because both RM and WM indicated that the subject should make the same arm choices. In an incongruent trial, the RM arms were open and baited in the study phase and left empty in the test phase (thus pitting RM against WM, each of which indicated a different behaviour to the subject). Accuracy was better for RM than for WM at 1-h and 24-h retention intervals (but not at 5 s) for congruent, but not incongruent trials. WM but not RM was found to decline over the 24-h retention interval. This study provides evidence that RM and WM are independent systems that can both facilitate and compete with each other.

Competition between WM and RM has also been found in birds. Roberts, Strang, & Macpherson (2015) used a symbolic delayed matching-to-sample task to examine the interaction between WM and RM in pigeons. Pigeons initially were trained on a symbolic delayed matching-to-sample task in which a coloured sample stimulus (red or green) had to

be matched with comparison stimuli (vertical or horizontal stripes). Once this task was learned to a high level of accuracy (at a 0-s delay), subjects were tested at several delays to establish a retention curve. The delayed matching testing was alternated with visual discrimination training, in which subjects always had to choose either vertical or horizontal stripes for reinforcement, in order to establish reference memory for the orientation of the stripes. The goal of this study was to determine the extent to which congruency and incongruency between comparison test stimuli and visual discrimination training stimuli would affect performance at different retention intervals. That is, if the subject was trained to choose horizontal stripes in the discrimination task for reinforecement, to what extent would this affect its behaviour on a delayed matching (working memory) trial in which the correct response was horizontal stripes (a congruent condition) versus a trial in which the correct response was vertical stripes (an incongruent condition)?   It was found that matching accuracy was high on both congruent and incongruent trials at short retention intervals of 0 or 1 sec. As the retention interval increased up to 10 s, however, the incongruent retention curve dropped below chance accuracy while the congruent retention curve remained high, showing that an initial dominance of WM was replaced by RM as WM weakened. This interaction was found in four experiments that manipulated the strength of WM and RM—strengthening either type of memory led to a decrease in the influence of the other.

A Different Approach to the Study of Spatial Memory in Dogs

Based on a concern that the radial maze is simply not the most valid way to approach the study of spatial memory in domestic dogs, the present study sought to use a different apparatus and procedure. Rather than having dogs search for food in the eight arms of the

maze, we had them search for food within the four corners of a large area (an empty classroom in Experiment 1, and an outdoor field in Experiment 2). Food items were hidden under plastic flower pots, which the dogs had previously been trained to knock over. Whereas the enclosed nature of the radial maze is undoubtedly foreign to a naïve pet, the idea of searching a large space for treats would seem to be a more natural and therefore an ecologically valid way to approach the study of spatial memory in dogs. This approach bears some similarity to the MacDonald et al. studies which successfully demonstrated spatial memory in yellow-nosed monkeys (MacDonald & Wilkie, 1990), marmoset monkeys (MacDonald et al., 1994), gorillas (MacDonald, 1994) and orangutans (MacDonald & Agnes, 1999).

The Macpherson and Roberts (2010) studies showed that like other animals in similar tasks, dogs perform better in a win/shift paradigm than in a win/stay paradigm—the win/stay condition was therefore dropped from this task. In the study phase of this experiment, flower pots were placed in two corners of the search area. Dogs were allowed to knock over these two flower pots (simulating a forced choice) and to consume the treats hidden underneath. The dogs were then removed from the room for a brief retention interval before the test phase. In the test phase, flower pots were placed in all four corners of the room, with food rewards hidden under the locations which were not baited in the study phase. This procedure is also unique in that it also tests dogs on both RM and WM within the context of a spatial memory task, and if successful could ultimately allow examination of the competition between WM and RM in a way that is similar to the Jacoby PDP studies, as well as other recent research with monkeys (Tu & Hampton, 2013), rats (Guitar & Roberts, 2015), and pigeons (Roberts, Strang, & Macpherson, 2015).

Experiment 1

Experiment 1 was conducted indoors, in a large empty classroom. Rather than hiding food in the extremities of a radial maze, food was hidden within the four corners of a large empty classroom. All dogs were randomly assigned one corner to be their RM corner, as well as a WM corner, which varied randomly among the other three corners from trial to trial. In the test phase of a trial, dogs could find a hidden food reward in the RM corner, as well as the WM corner. Because dogs have been shown to use a win/shift strategy (Macpherson & Roberts, 2010), dogs therefore found food rewards in the *opposite* two corners in the study phase of the trial. Dogs were tested for their ability to recall the locations of both the RM and WM corners, based on the order in which the dogs visited each corner in the test phase of the trial. For example, if a dog was assigned corner #4 as its RM corner, and corner #2 as its WM corner on a particular trial, then in the study phase, it would find a food reward in corners #1 and #3, while in the test phase, it would find food in corners #4 and #2. In subsequent trials, corner #4 would continue to be the correct RM corner, but the correct WM corner would vary randomly among corners #1, #2, and #3.

Method

Subjects.

Six dogs of various breeds were tested. These included two rough collies (Cash and Sedona), two whippets (Jasper and Finnegan), a goldendoodle (Cally) and a labradoodle (Ollie). Four of the dogs were male and two were female. The dogs were all pet dogs volunteered for the study, and ranged in age from 10 months to 5 years (mean age of 2.79 years). All dogs had received basic obedience training and had vaccines in good standing.

As noted in the previous chapters, Cash and Sedona belong to the author of this paper. As such, the author was not involved in testing either Cash or Sedona on this task, and it is not believed that their relationship with the author had any effect on their performance in this task.

Materials.

The experiment was conducted indoors in an empty, well-lit classroom measuring 13.7 m x 8.5 m. A plastic flower pot was placed in each corner of the room, along with a platform created by taping two bricks together with duct tape (see Figure 1). This platform ensured that the dogs would knock the flowerpot over to find a hidden food reward, rather than just push the flowerpot around the room.

Procedure.

Prior to testing, each dog was trained to knock over a flower pot in order to find a hidden food reward. This training took approximately 20 min per dog. Once this training was complete, experimental trials were conducted. Dogs were typically tested for 40 min at a time, 2-3 times per week (scheduling was based on the owner's availability to bring the dog in, and so scheduling was slightly variable across subjects).

In the study phase of a trial, two flower pots were placed in two corners of the room. A food reward (a piece of cheese) was placed upon the brick platform beneath the flowerpot. Additional pieces of cheese were hidden under the platform in order to control for olfactory cues. Each dog was assigned randomly to a RM corner—this corner was never baited in the study phase of the trial, and always baited in the test phase of the trial. Dogs were also assigned a WM corner, which varied among the remaining three corners from trial to trial.

Figure 8 Flowerpot and brick base used in both Experiment 1 and Experiment 2.

At the beginning of the study phase, the dog was walked to the center of the room by the experimenter and released. The dog was allowed to visit each of the two available flower pots, and to knock these flower pots over to obtain the food reward underneath. The two non-baited corners were empty, as the flower pots and platforms were removed entirely for the study trial. Once the dog depleted the two flower pots, the experimenter walked the dog out of the room, where the dog was minded by a second experimenter. A retention interval of 1 min then elapsed, while the experimenter set up the flower pots for the testing phase. In the testing phase, platforms and flower pots were set up in all four corners, although only the RM corner and the unvisited WM corner actually contained a food reward. Once all four flower pots were in place, the experimenter returned the dog to the center of the room, and again released the dog. The dog was allowed to visit each corner of the room until both the RM corner and WM corner had been depleted.

Results

Dogs' performance was measured in two ways: rank of corner selection (how soon the dog visited the RM and WM corners) and number of correct choices in first two corner selections (if a dog performed the task perfectly, then both the RM and WM corners would be visited in its first two corner selections). Means for the RM rank ($M = 2.17$) and the WM rank ($M = 2.16$) were nearly identical. Mean ranks for individual subjects (see Figure 4.2; upper panel), however, show that three subjects (Cash, Ollie, and Cally) tended to go to the RM corner before the WM corner, while the other three dogs (Sedona, Jasper, and Finnegan), went to the WM corner sooner. Overall, dogs chose to visit the WM corner $t(5) = 4.52$, $p = .006$, but not the RM corner $t(5) = 2.16$, $p = .08$ sooner than they would have by chance (chance rank was 2.5).
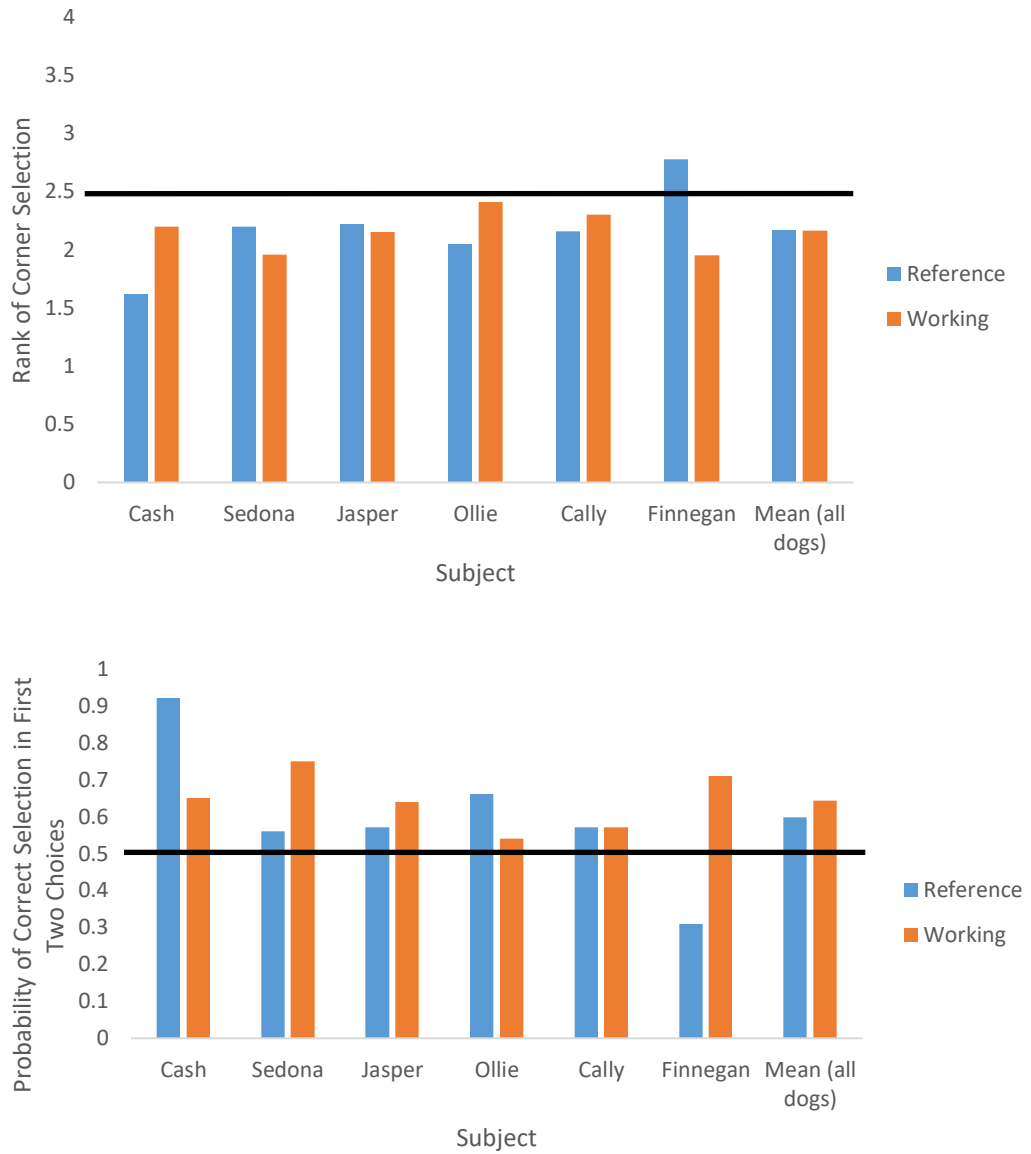
Figure 9. (A; Upper Panel) Rank of corner selection for RM and WM for all subjects in Experiment 1.

(B; Lower Panel) Probability of selecting RM and WM corner in first two corners selections for all subjects in Experiment 1. The horizontal lines represent chance performance (rank of 2.5 and probability of .50).

Means for the number of correct choices in the first two selections for the RM corner ($M = .6$) and the WM corner ($M = .64$) were also similar (see Figure 4.2; lower panel). Two dogs (Cash and Ollie) more often chose the RM corner in their first two selections than the WM corner, while three dogs (Sedona, Jasper and Finnegan) more often chose the WM corner in their first two selections. One dog (Cally) was just as likely to visit the RM corner as the WM corner in her first two choices. Overall, dogs were above chance (chance was .5) in choosing the WM corner $t (5) = 4.39$, $p = .007$, but not the RM corner $t (5) = 1.22$, $p = .27$ in their first two choices.

The failure of t-tests for RM to reach significance is surprising. Given that the RM corner remained the same for every trial, one would expect this location to be more easily remembered and more frequently visited by the dogs. One subject in particular (Finnegan), very often did not choose the RM corner as one of his first two corner selections; this pattern is inconsistent with the behaviour of the other subjects and resulted in the failure of the t-test for RM to reach significance.

Discussion

While means for both rank of arm selection and number of correct choices in the first two selections were mostly above chance, individual differences in performance were apparent across subjects. One possibility is that the flower pots were too close together, making the task too easy for the dogs. Given that the dogs had a 50% chance of obtaining a reward when choosing at random, and little effort was required to travel from one flower pot to the next, the dogs may simply not have been motivated to attempt to remember the correct locations, choosing instead to search (at least in part) at random. For example, it was often observed that a dog would make a seemingly deliberate choice to go to either the RM or WM corner in its first selection, and then simply go to the nearest flower pot in front of it for its

second choice. The procedure therefore might benefit from a larger arena, in which the dogs would have to exert more effort in making a corner selection. Taking this measure might compel the subjects to rely more on their memory in making a choice.

<div style="text-align:center">Experiment 2</div>

Experiment 2 was similar to Experiment 1, with the exception that it was conducted both indoors (in the same classroom used for Experiment 1) and subsequently outdoors, in a large field. Outdoors, the four flowerpots were placed 12.19 m apart, in a square formation. The use of a larger search area in this experiment forced subjects to travel farther (and thus exert more energy) in order to search a corner for a food reward. It was anticipated that requiring the dogs to exert more effort in order to complete the task would encourage them to use memory in order to solve the task, rather than selecting corners at random. Additionally, in order to examine how well memory for the RM corner and WM corner could be recalled after a delay, retention intervals were added between the training and test phase, such that dogs waited 5, 15, 30 or 60 min before returning for the test phase. Presumably, recall for the RM corner (which remains consistent for each dog across trials) should remain intact across trials, while memory for the WM corner (which varied randomly across trials) should decay as the retention interval increases.

Method

Subjects.

Cash and Sedona, the two rough collies from Experiment 1, served as the only subjects in this experiment. Given the outdoor nature of this experiment, it was impossible for their owner, the author of this study, to be completely out of sight while testing. The author recorded their data from a point 10 m away, while wearing dark sunglasses and

looking down at a clipboard. Given that both dogs were motivated and engaged by the task, and that their owner stood 10m away with her eyes obscured by sunglasses, it is not believed that her presence had any effect on the dog's performance.

Materials.

The same flower pots and brick platforms that were used in Experiment 1 were also used in Experiment 2. Additionally, each platform and flowerpot was placed upon a plywood board measuring 0.6 m x 0.6 m. These plywood boards had metal clips attached, which could fix the flower pot in place. In the test phase of a trial, the two incorrect options (those which were neither the RM nor the WM corner) had the flower pot fixed in place, making it impossible for the dog to knock the flowerpot over. This was another measure taken to make the task more difficult for the dog, and hopefully to make an incorrect choice more salient and perhaps frustrating to the subject.

Procedure.

The task used in Experiment 2 was the same as that used in Experiment 1, with the exception that dogs were randomly given retention intervals of 5, 15, 30, or 60 min between the training and test phases. When trials were conducted indoors, subjects waited in an adjoining office during the retention interval. For outdoor trials, dogs waited in a nearby vehicle during the retention intervals. In the test phase of each trial, the experimenter also ensured that the flower pots in the two incorrect corners were clipped in place, such that the dogs would be unable to knock over the flowerpot if they made an incorrect selection. Trials were limited for both the indoor (between approximately 20-40 trials) and outdoor (20 trials) version of this task.

Results

      Means for the collies show that in both the indoor (see Figure 4.3) and outdoor (see Figure 4.4) scenarios, Cash showed a clear preference for visiting the RM corner sooner than the WM corner. These curves overlap much more for Sedona, with the exception of the 30 min retention interval, where she shows a preference for visiting the RM corner before the WM corner in both the indoor and outdoor scenarios. Likewise, the performance of the collies was also consistent both indoors (see Figure 4.5) and outdoors (see Figure 4.6) when considering their accuracy for choosing the RM and WM corner within their first two corner selections. Cash was always more likely to choose the RM corner in his first two corner selections than the WM corner. His performance on this task was highly accurate (particularly for the RM corner) and dropped off dramatically only at the 60-min retention interval. Although it makes sense that his memory for the WM location would drop, it is unclear why he would experience difficulty finding the RM corner after this delay. Sedona again had overlapping curves, but strangely seemed to improve in her accuracy for recalling the WM corner at the 60-min retention interval. Given the limited number of outdoor trials, however, this finding may be the result of chance fluctuation in performance.

Discussion

      Both collies performed consistently across the indoor and outdoor testing scenarios. This suggests that the additional measures of making the flower pots further apart and fastening flower pots in place for incorrect responses did little to encourage the dogs to rely more upon memory in making their selections. Like in Experiment 1, however, there was a lack of consistency in how the individual subjects performed on the task, though both subjects demonstrated some spatial memory ability. These individual differences in subjects

Cash (Indoors)

Sedona (Indoors)

Figure 10 Rank of corner selection for RM and WM (indoors) with both subjects in Experiment 2. The horizontal line represents the chance rank.
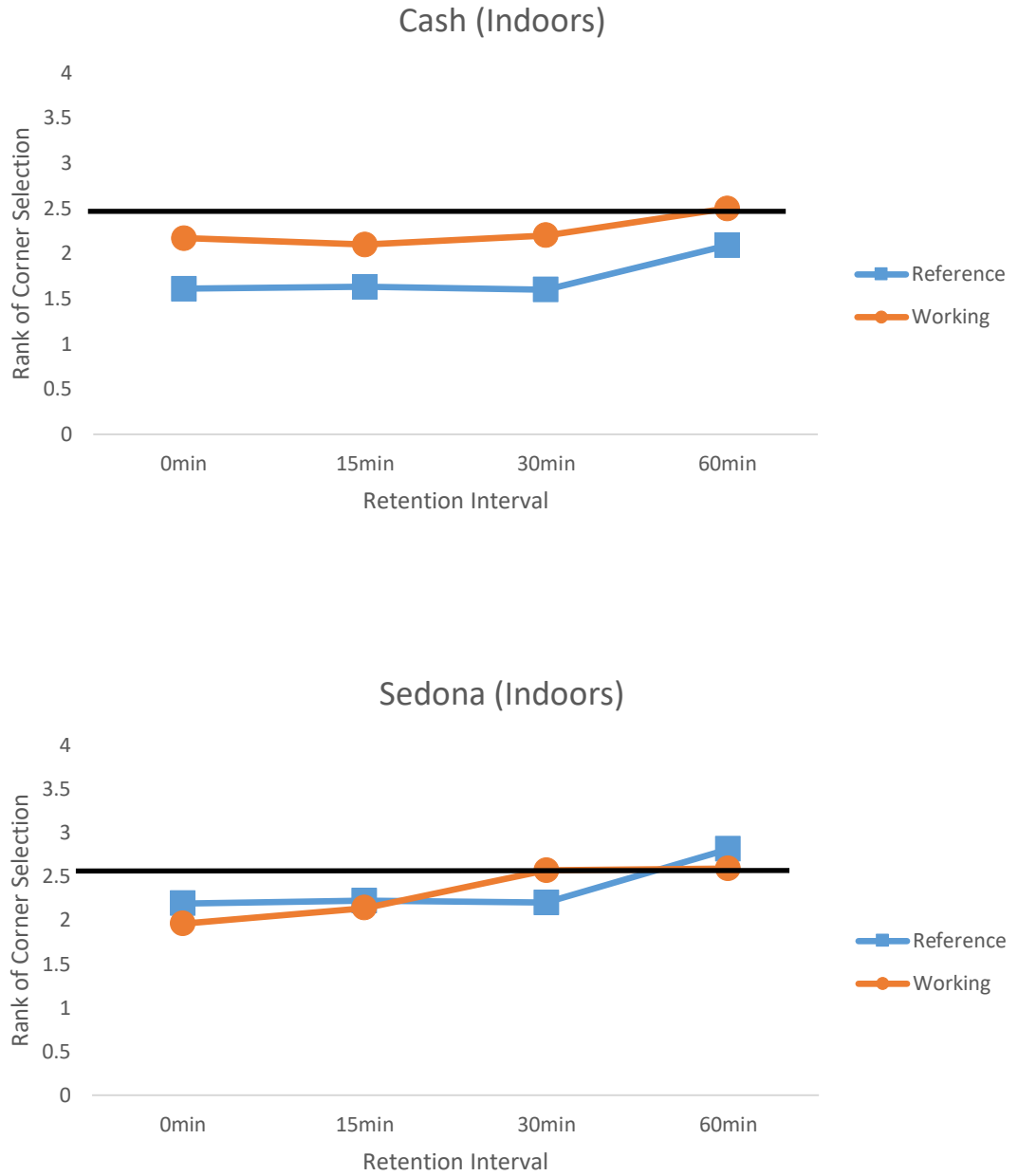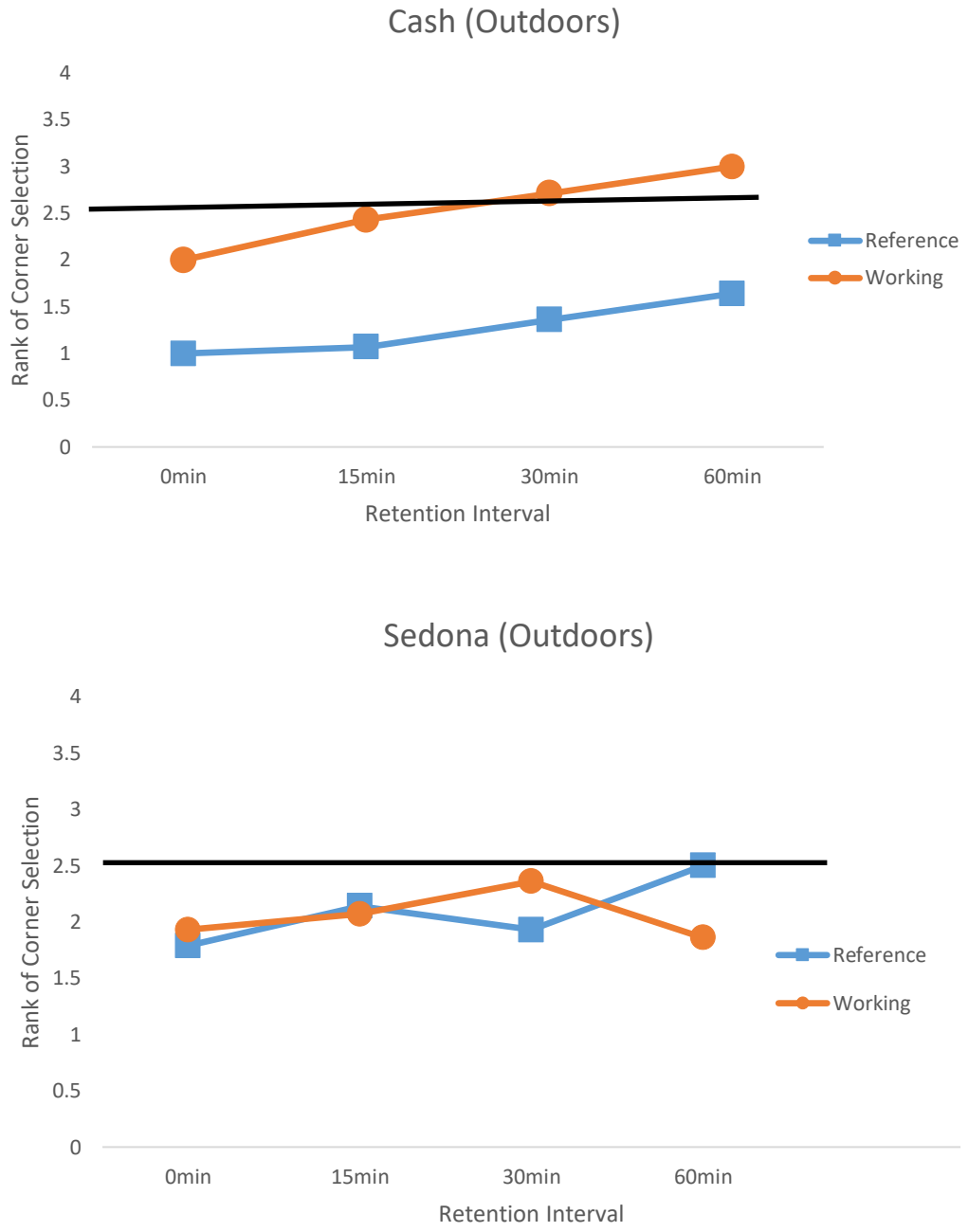
Figure 11 Rank of corner selection for RM and WM (outdoors) with both subjects in Experiment 2. The horizontal line represents the chance rank of 2.5.

Figure 12 Probability of selecting RM and WM corner in first two corners selections for both subjects (indoors) in Experiment 2. The horizontal line represents the chance proportion of .50.

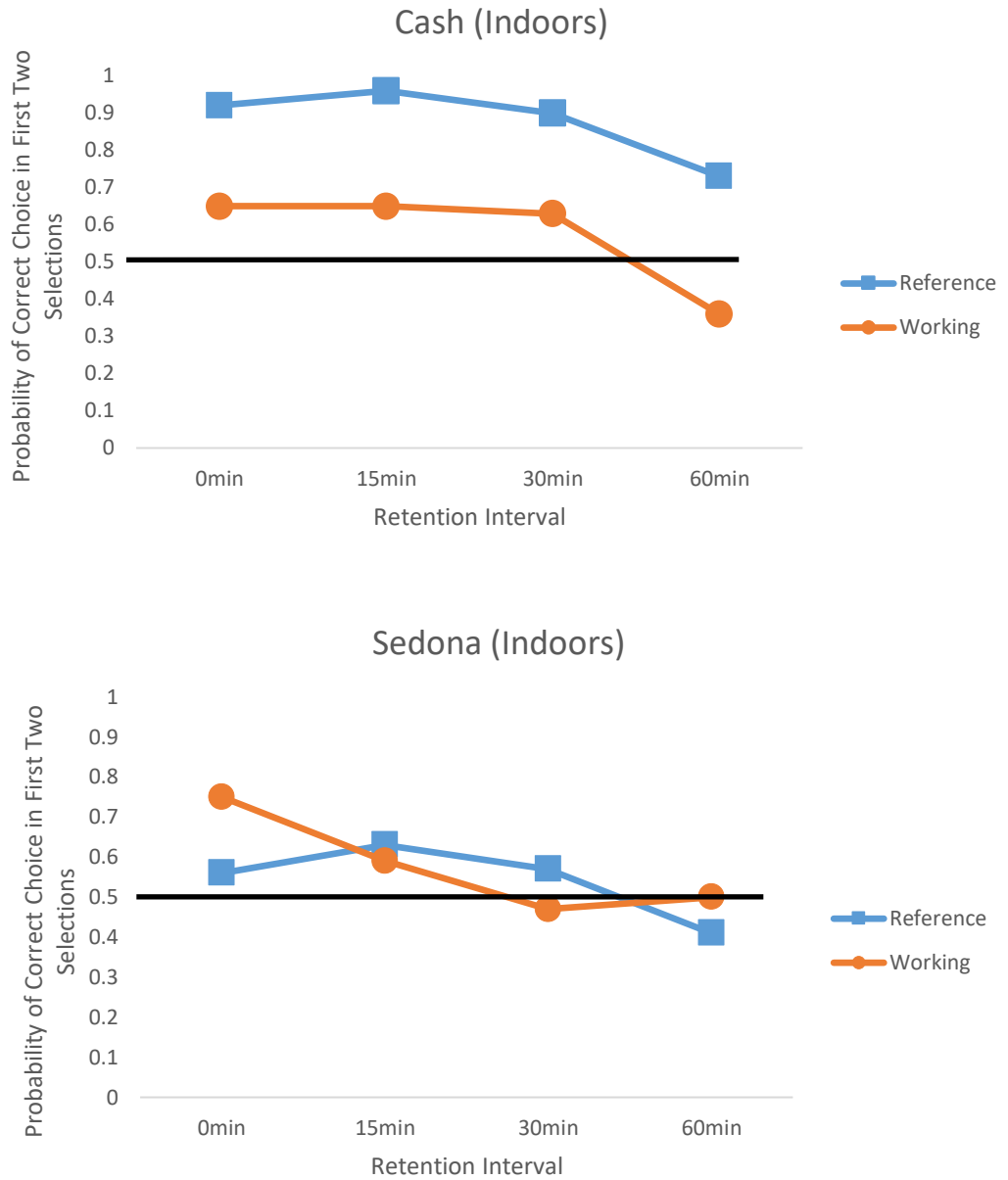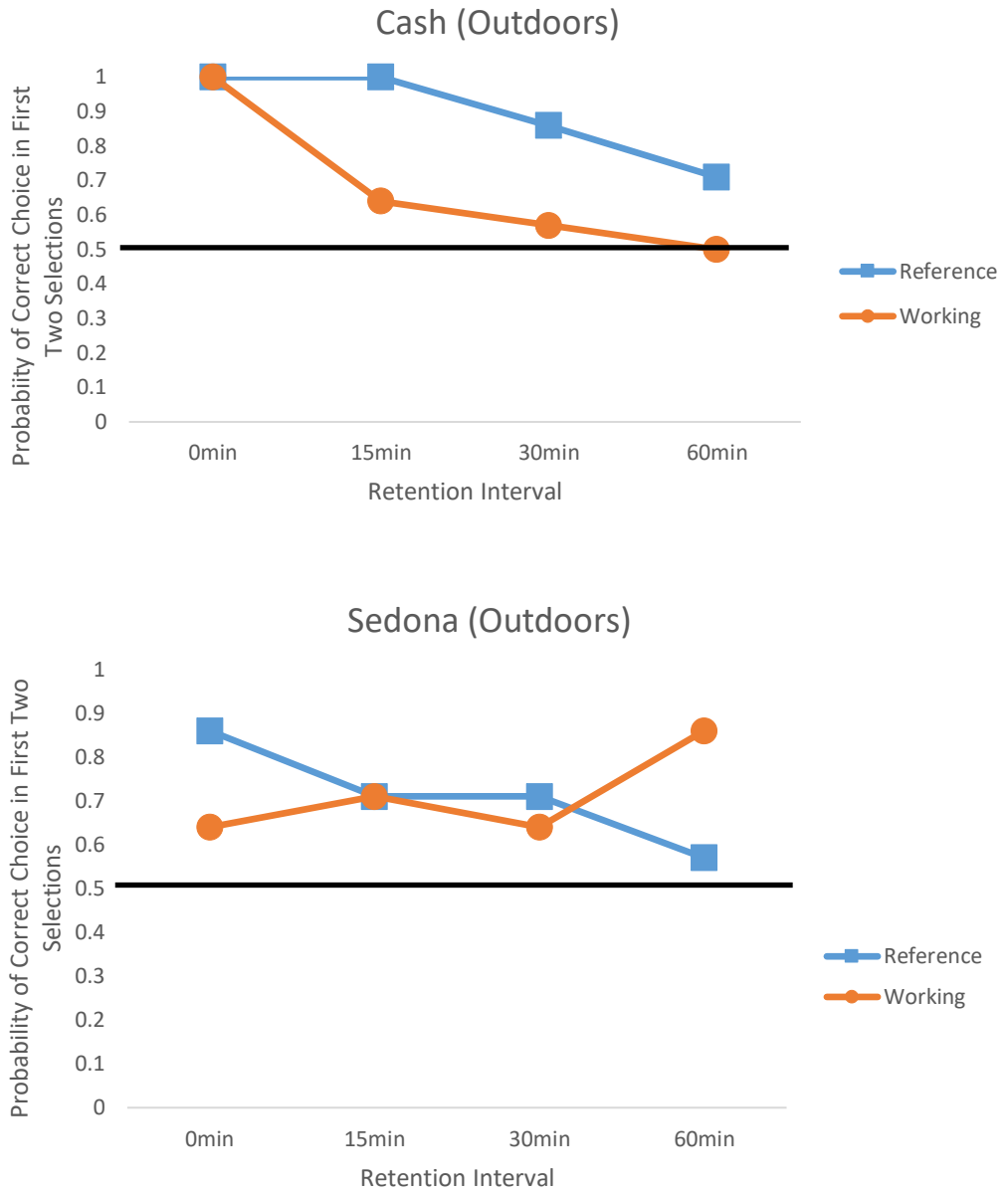*Figure 13* Probability of selecting RM and WM corner in first two corners selections for both subjects (outdoors) in Experiment 2. The horizontal line represents the chance proportion of .50.

should be given further consideration in the design of future studies—the development of a measure of food motivation, attention, and/or activity level, for example, may facilitate finding subjects that remain interested and more consistently engaged in the task across many trials.

General Discussion

The present studies suggest, like our previous (Macpherson & Roberts, 2010) spatial memory studies, that dogs have at least some spatial memory ability. Performance, however, was extremely variable across subjects. One subject (Cash), was particularly good at this task, and became quite accurate in finding both the reference and working memory corners, with his performance dropping dramatically only at the 60-min retention interval. Cash's temperament likely played a role in his adeptness for this task (at the time of this writing, Cash has been used in several different experiments and has excelled in all of them). While Cash is food motivated, he is more interested in attention from humans, making him very attentive during testing, without being overly anxious about obtaining food. Cash is also a rough collie—a breed descended from the ancient sighthounds. Collies are more visually-oriented, given their descent from sighthounds and origin as sheepdogs. Unlike sighthounds (which tend to be more independent or even standoffish), however, collies are generally very attentive to humans.

The traits that seem to make Cash an ideal subject raise an important issue—dogs are highly variable, both in terms of physical traits and temperaments. Additionally, they are often raised with varying levels of training and attention from their owners—some dogs may live in the city and have been taken to many obedience classes, while others may live in a rural area where they do not encounter the public often and may have little need for formal

training. This is vastly different from similar studies with rats and pigeons, where these animals are nearly identical in type and temperament, and are raised in a laboratory setting. Further studies of spatial memory in dogs are worth pursuing because there is a bounty of research questions that have yet to be addressed. One of these questions is how best to approach the study of spatial memory in dogs given the vast breed and temperament differences in this species.

While subjects demonstrated some use of spatial memory, there was overall a lack of consistency in behaviour across individuals, and overall the dogs' performance was not as accurate as that typically found with rats. One interpretation of these results is that through intense selective domestication, dogs may have lost spatial memory abilities that might be found in their wild ancestor, the Gray wolf (Frank & Frank, 1982). Evidence supporting this interpretation has been provided by Kruska (2005), who, based on allometric comparisons (comparisons of brain to body size relationships), concluded that domestication leads to significant reduction in brain size, particularly in larger carnivores. Kruska's data show that the dog brain has lost 30% of its size through domestication. Furthermore, the hippocampus, a brain structure that is widely thought to play an important role in spatial cognition, has been reduced in size by 41% in dogs, as a result of their domestication. These findings are particularly surprising when considered in light of data provided by Kruska for other species. Lab rats, for example, are domesticated from wild rats but have lost only about 10% of overall brain and hippocampus size. Given the small sample size (N = 2) of the present study, however, any interpretation of these data should be treated with caution.

A test of the hypothesis that dogs have lost spatial memory abilities found in wolves as a result of their domestication would require testing wolves on comparable spatial memory

tasks. Further testing of dogs' spatial memory ability will be necessary before any firm conclusions can be reached. It may be that dogs were tested under conditions that were not favourable to a demonstration of their true spatial memory ability (Bitterman, 1960). For example, dogs were not deprived of food before testing, as rats are in most radial maze experiments. Given that they would soon be fed by their owners anyway, it is possible that the dogs were not as motivated to engage in this task.

Context in Working and Reference Memory

Context has emerged as another variable of interest in understanding the relationship and interaction between reference and working memory. Roberts, Strang, and Macpherson (2015) alternated a symbolic delayed matching-to-sample task with pigeons (where subjects had to match red or green lights to vertical or horizontal stripes) with a discrimination task (in which subjects had to always choose either vertical or horizontal stripes) in order to examine the interaction between working memory and reference memory in pigeons. An interaction was found between WM and RM, indicating that strengthening either type of memory leads to a decrease in the influence of the other.

In a follow-up study, Roberts, Macpherson, and Strang (2016) used the same procedure, in which pigeons were tested with visual discrimination training (using vertical and horizontal stripes) and symbolic delayed matching-to-sample (using blue and white lights as sample stimuli). Additionally, during delayed matching WM training, the chamber was bathed in red light for 1 s before presentation of the test patterns and remained on until a choice has been made. On RM training sessions, the chamber was bathed in green light for 1 s before and during choice between the test stimuli. Thus, different colored contexts were presented on WM delayed matching tests and on RM tests. Delayed matching was then

tested at retention intervals of 1, 3, 6, and 10 s, and retention curves were examined separately for congruent and incongruent trials when the WM context was presented and when the RM context was presented. Strong competition between memory systems now disappeared. In the WM context, there was no difference between retention curves on congruent and incongruent trials. In the RM context, the stimulus reinforced on discrimination training trials was chosen on both congruent and incongruent trials, with no effect of the retention interval. When different contextual cues were used, working memory was completely protected from reference memory interference. It was argued that context provides access to different memory systems.

The influence of context has also been examined in rats. Roberts, Guitar, Marsh, and MacDonald (2016) conducted an experiment in which rats were given both WM and RM trials on an 8-arm radial maze. A win/stay procedure was used for RM trials (meaning that rats would find food rewards consistently in the same four locations in both the study and test phase), whereas a win/shift procedure was used for WM trials (meaning that rats would find food rewards in four locations for the study phase, and the four opposite locations for the test phase). Tests were conducted using congruent and incongruent conditions at retention intervals of 15 s, 15 min, and 30 min. At the 30-min retention interval, a congruency effect was found such that more forgetting appeared when the WM arms were incongruent with the RM arms. In a second experiment, context was also manipulated by altering the brightness and tactile surface of the maze. Some trials were conducted on the maze with smooth, light grey coloured arms, while other trials were conducted with a rough, black tactile surface added to the arms. Consistent with previous findings, rats performed better when WM and

RM were congruent than when they were incongruent. Additionally, placing rats in the WM context in the test phase led to overall better retention than placing tats in the RM context.

Unlike the findings from experiments with pigeons (Roberts et al., 2016), placing rats in the WM context in the Roberts et al. (2016) study did not eliminate the effect of congruency, and placing the rats in the RM context did not eliminate the effect of of the retention interval. While pigeons are known to be very sensitive to coloured light, it is not known whether the brightness and texture cues used on the radial maze study were as readily used by rats. One possible explanation for the difference in these findings may be that the contextual cues used were simply more salient for the pigeons than were those for the rats. Regardless, the use of contextual cues to possibly preserve memory continues to be an interesting research question, which could also be addressed in future studies of memory in dogs. Given that dogs have been found to be highly sensitive to auditory cues (Macpherson & Roberts, 2017), for example, one possibility may be to manipulate the frequency or intensity of a tone as a contextual cue for dogs.

Food Caching as a Possible Paradigm for the Study of Spatial Memory in Dogs

Result of the present study were mixed—and like the Macpherson and Roberts (2008) radial maze study, this paradigm may not be the ideal approach to the study of spatial memory in dogs. Food caching paradigms, however, have yielded a bounty of findings in various species of food caching birds (e.g.: scrub jays (Clayton & Dickinson, 1998); Black-capped chickadees (Hitchcock & Sherry, 1990); Clark's nutcrackers (Kamil & Balda (1985)). These food caching paradigms have often been used to address spatial memory, and more broadly "episodic-like" memory; that is, a non-human animal's memory for "what", "when" and "where" an event took place (minus exploration of the "autonoetic" consciousness

described by Tulving (1985) in his theory of human episodic memory). The procedure in these studies typically involves allowing a subject to cache items of food in a testing area; the subject is then returned to the testing area after a period of time in order to recover the food items, and the animal's accuracy for recovering these items is measured. Given that both feral and pet dogs are known to engage in caching behaviour, such a paradigm could be useful in both the study of spatial and episodic-like memory in dogs.

Presently, the issue of food caching in dogs has yet to be formally addressed by research, although it has been observed in numerous other canid species, including both wild (Harrington, 1981) and captive (Phillips, Danilchuk, Ryan & Fentress, 1990) wolves (*Canis lupus*); wild (Macdonald, 1976; Macdonald, Brown, Yerli, & Canbolat, 1994) red foxes (*Vulpes vulpes*); wild (Frafjord, 1993) arctic foxes (*Vulpes lagopus*); and captive (Phillips, Ryan, Ponilchuk, & Fentress, 1991) Coyotes (*Canis latrans*). Not all members of canid species, however, engage in consistent caching behaviour (Gadbois, Sievert, Reeve, Harrington, & Fentress, 2015); it therefore remains to be determined whether or not a food caching paradigm would be effective in the study of spatial memory in dogs.

Dogs as a Model for Human Memory Decline

The study of spatial memory in domestic dogs may have important implications for the study of human memory, as dogs show a pattern of cognitive decline similar to that observed in humans (Adams, Chan, Callahan, & Milgram, 2000B; Studzinski et al., 2006). Similarities in behaviour have been found between geriatric dogs and humans with Alzheimer's disease (Rofina et al., 2005). In one study (Pugliese et al., 2007), a significant correlation was found between amyloid-beta plaque maturation (a suspected marker of cognitive decline in humans) and cognitive decline in dogs.

Humans show neuron loss within the hippocampus and entorhinal cortex as a function of age. In one study, Siwak-Tapp et al. (2008) analyzed the brains of five young (3.4-4.5 years old) and five old (13-15 years old) dogs, and found that like humans, the older dogs experienced a significant loss of neurons in the hippocampus (though not in the entorhinal cortex). Futhermore, when dogs' daily routines were enriched with toys, pair housing, and increased outdoor walks, the loss of neurons was significantly reduced—suggesting an important role for social and behavioural enrichments in reducing cognitive decline. Taken together, these studies suggest that dogs make a promising model for the study of cognitive decline in humans, though a better understanding of memory processes in the domestic dog is needed to advance this research.

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Chapter 5

General Discussion

The domestic dog has greatly increased in popularity as a subject of study in comparative cognition over the past 20 years. Given the unique history between dogs and humans, it is unsurprising that the majority of these studies have focused on elements of social cognition, with both phylogenetic (Hare, Brown, Williamson, Tomasello, 2002; Hare & Tomasello, 2005; Miklósi et al., 2003) and ontogenetic explanations (Udell, Dorey, & Wynne, 2008; 2010) proposed by numerous researchers. While debate still exists as to exactly how dogs arrived at their unique cognitive skillset, two themes appear to consistently emerge from the collective data—one of which is that dogs are extremely good at tasks which involve acting on human cues (Hare & Woods, 2013). Examples of such tasks include object-choice tasks with the use of human pointing gestures or cues (Hare & Tomasello, 2002; Miklósi et al., 1998), detour tasks (Pongrácz et al., 2001), and tasks involving choice between an informative vs. non-informative human (McMahon, Macpherson, & Roberts, 2010; Petter, Musolino, Roberts, & Cole, 2009). The other, perhaps less-intriguing trend is that dogs are often lacking at tasks which require them to act independently of humans. These include their failure to seek help for a human who appears to be in distress (Macpherson & Roberts, 2006), as well as their difficulty in information-seeking tasks which are not human-directed (McMahon et al., 2010). Dogs also appear to fail to understand means-end connections without extensive training, such as the string-pulling task (Osthaus, Lea, & Slater, 2005).

The interest in social cognition with respect to the domestic dog is intuitive, given our close relationship with these animals. In our enthusiasm to understand the relationship between dogs and humans, however, it may be the case that the field of dog cognition has overlooked some aspects of basic cognition. While hundreds of empirical papers can be

found on various topics pertaining to social cognition in domestic dogs, only a handful of papers can be found on topics related to basic cognitive processing in this species. This paucity of dog articles seems strange given that areas such as interval timing, numerical discrimination, and spatial memory have been overwhelmingly important areas of study in comparative cognition as a whole, with hundreds of papers dedicated to these topics, across many journals, and using a number of other species. To truly study dogs through the lens of comparative psychology, it seems reasonable that we should establish an understanding of basic cognitive processing that is at least somewhat on par with what has been demonstrated with other species. In light of this, the preceding chapters were dedicated to the study of interval timing, numerical discrimination, and spatial memory, as these three dimensions of cognition appear to be common to most animals as fundamental skills in navigating day-to-day life. From a practical perspective, it also makes sense to develop appropriate apparatus for the study of these phenomena in dogs, as the typical apparatus of choice in other species (often the radial maze or operant conditioning chamber) will not typically work with dogs.

Results from the present studies show that dogs, like other animals, appear to be sensitive to both number and time. Dogs demonstrated the ability to discriminate number (when stimuli were presented simultaneously), and were also successful in timing a fixed interval. Probe trials were also given in order to generate peak time curves, yielding scalloped data patterns which are the signature findings of such studies (Roberts, 1981). In both cases, the performance of the dogs was consistent with a ratio-dependent explanation of behaviour.

In discriminating number, dogs' accuracy decreased as S/L ratios approached 1.0 in the simultaneous counting studies, demonstrating effects consistent with Weber's Law.

Interestingly, no ability to discriminate number was found across a variety of different tasks in which food items were presented sequentially. This failure to discriminate was likely because in the sequential task, choices were reinforced even when they made an error (albeit with less food than if they had made the correct choice). This interpretation is supported by the observation that dogs almost always responded correctly when given a ratio of 1vs.0 (in which case there is no reward for making an incorrect choice). Additionally, sequential counting tasks are more working memory driven than simultaneous tasks (as dogs must remember what they saw at the first bucket and mentally compare it to what they see at the second bucket). Monkeys have also been shown to perform better in simultaneous counting tasks rather than sequential tasks (Nieder, Diester, & Tudusciuc, 2006). It is likely that both reinforcement and working memory capacity play a role in dogs' performance in these tasks, and future studies could tease apart the influence of each.

It is worth noting that in the years since the data from these numerical tasks were collected and subsequently published (Macpherson & Roberts, 2013), other studies of quantity and/or numerosity in dogs have emerged. Horowitz, Hecht, & Dedrick (2013) found that dogs failed to discriminate different quantities of food by olfaction alone—the subjects did, however show preferential attention to the larger quantity when initially investigating the items, which were presented on closed plates. Petrazzini and Wynne (2016) pitted number of food items against overall quantity of food, and found that dogs based their choice on the total amount of food rather than the number of food items. The Horowitz et al. (2013) and Petrazzini & Wynne studies, however, used food items as the stimuli to be discriminated, whereas Macpherson and Roberts (2013) used non-food items in a simultaneous counting

task. Future studies may consider the use of different types of stimuli to determine in which contexts numerical information is more relevant than quantity information, or vice versa.

Results from the spatial memory studies are less clear-cut and may be considered an informative guide in the design of future studies of spatial cognition. While some dogs tended to approach the RM corner before the WM corner, other dogs did the opposite. Even with the addition of retention intervals and outdoor trials which required more physical effort on the par of the dogs, performance was inconsistent across subjects (though all dogs did appear to demonstrate some use of spatial memory). The high degree of variation among subjects in the spatial memory task suggests that although dogs likely have good reference and working memory, this experimental task was not the right one to address this question. Individual motivation seemed to play a role here, with some dogs appearing to be more attentive to the task than others. While individual differences across subjects were most problematic for the spatial memory studies, differences between dogs were seen in all three sets of studies reported here and will be discussed in further detail.

Recently, another attempt was made at addressing the question of memory in dogs, this time using an olfactory task (Lo, 2017). Dogs were trained with 20 different pairs of odours. Within each trial, the dogs were presented with four covered containers. Three of these containers had the scent of the S- on the lid (and were empty), while one lid had the scent of the S+ (and a food reward inside). Dogs were trained to a 75% criterion on each of these odour sets, before ultimately being presented with a final memory test (which tested them for their memory of each of the 20 odour sets). Even months after learning the initial odour sets, dogs were highly accurate on the memory test. Further studies using this task are

currently underway, and present what is likely a very promising approach to the study of reference memory in dogs.

Individual Differences in Subjects

At a glance, the area of canine cognition may be appealing to potential researchers—dogs are everywhere, and many dog owners are very keen to have their dogs involved in behavioural research. Dog research also tends to generate public interest in a way that research with more typical laboratory species does not, resulting (for better or for worse) in increased media coverage. The logistics of running a sound study in dog cognition, however, are often a different matter. Unlike rats and pigeons, dogs come in all shapes and sizes, making the construction of an apparatus or determining distances to be travelled in a procedure more difficult. Additionally, there are often differences in structure and function, training (or lack thereof) and motivation which can make testing dogs a difficult task.

Breed Structure and Function.

Dogs come in a wide variety of shapes and sizes, largely due to selective breeding. The American Kennel Club (AKC) and Canadian Kennel Club (CKC) recognize 202 and 175 breeds, respectively, and the Fédération Cynologique Internationale (FCI), the largest internationally recognized registry of dogs, currently recognizes 332 breeds. Worldwide, however, there are many other breeds of dog which are not formally recognized by these clubs. Purebred dog registries have a standard for every breed of dog they recognize—these standards describe what the conformation and temperament of these breeds should be, and breeders strive to produce dogs that are as close in type to these standards as possible. Breeds of dog are also assigned to particular groups, along with other breeds which were developed for a similar purpose (the exception to this rule in both the AKC and CKC is the

non-sporting group; breeds belonging to this group are highly variable in their structure and function). Both the AKC and CKC currently recognize seven groups of dogs, these being the sporting, hound, working, terrier, toy, non-sporting and herding groups. Even within a particular group, there is some variation in the types of jobs which dogs perform. For example, the hound group contains both scent hounds and sight hounds. Scent hounds tend to have large floppy ears and larger noses for tracking prey by scent (ex: beagles, bloodhounds), and are primarily of British origin. Sight hounds (ex: greyhounds, salukis) tend to be tall, lean, fast, and have long lean heads which make them ideal for tracking prey visually across desert terrain—they were developed primarily in Egypt and the Middle East. Likewise, the sporting group consists of various types of gun dogs, retrievers, and spaniels. In the herding group, some breeds were developed to actively herd livestock, while others were developed to stand guard over the livestock, becoming active only when a predator or threat is present.

The differences in structure and function among different breeds of dog may have important implications for studies of dog cognition. For example, the rough collies used in the numerical discrimination tasks described in Chapter two were likely a good choice of subject—rough collies were bred to herd sheep, a task which is highly visual. This was fortuitous given that the procedure for the experiments required attention to visual stimuli. If we had conducted this task with beagles, a scent hound, it is possible that this breed's predisposition to track odor would make it more difficult for them to focus on a visual task. Any difference between the performance of the hypothetical beagles vs. the actual performance of the collies would likely be the result of perceptual differences rather than cognitive differences.

Breed differences are not simply functional (that is, a product of a breed's aptitude to do the job for which they were bred). Selective breeding across years for particular jobs has resulted in at least some perceptual differences across breeds. Skull length, for example, is positively correlated with retinal ganglion cell topography (Miller & Murphy 1995; Peichl, 1992), such that dolicocephalic breeds (breeds with long skulls, ex: rough collies, greyhounds) have retinal ganglion cells arranged in a visual streak across the retina, while brachycephalic breeds (breeds with short skulls, ex: Pekingese, pugs) have retinal ganglion cells clustered in a single point (structurally this more closely resembles the human fovea, with the exception that humans have far more retinal ganglion cells, resulting in superior visual acuity). The differences in retinal physiology suggest that long-headed dogs (which tend to be those bred to track objects or prey visually) may be more sensitive to visual stimuli at a distance or on the horizon, while short-headed breeds are more sensitive to seeing objects directly in front of them. Likewise, clear differences in olfactory physiology exist across breeds, with the broader nosed scent hounds having larger nasal cavities and more receptor cells dedicated to olfaction than breeds not meant to track by scent (Horowitz, 2016). Many of these breeds (ex: basset hound, bloodhound) also have very long ears, which are thought to help "trap" a scent around the dog's nose, as well as loose lips—the saliva from which is yet another mechanism to trap odor molecules.

Breed differences are not limited to physical structure. Differences in temperament across breeds are also the result of selective breeding. Ancient breeds (some of which date back thousands of years) tend to be more independent, while "newer" breeds are among the more gregarious (likely in part because dogs have increasingly been bred for companion purposes). These temperament differences are consistent with findings from studies of the

dog genome, which found genetic subdivision between ancient breeds, and those developed since the 19th century (Pollinger et al., 2010).

While fundamental cognitive skills should be relatively similar across all breeds of dog (as they are all members of a single species), it is clear that structural, functional and perceptual differences do exist among different breed types and should likely be taken into consideration when designing studies of dog cognition. In many parts of the world, however, dogs are feral and thus not subject to the same selective pressures. Coppinger and Coppinger (2001) describe these dogs as "village dogs" that may be thought of as the average or prototypical dog. They weigh approximately 30 pounds, are of average build, medium muzzle, and moderate coat. They are large enough to scavenge or catch small prey but small enough to survive on minimal calories. Importantly, these dogs tend to be minimally reliant on humans—some may be fortunate enough to have humans leave food out for them, but others exist completely independently of humans. Studies of dog cognition repeatedly find that dogs: A.) are excellent at tasks involving human cues; and B.) are less successful in tasks where they have to act independently. Dogs in these studies, however, are typically pet dogs which have been raised with extensive human socialization. It would be interesting to determine whether or not these less socialized counterparts have an advantage on tasks that require more independence.

Personality Differences in Dogs?

One of the earliest and most well-known attempts at identifying breed-differences in behaviour is represented by the work of Scott and Fuller (1965). Scott and Fuller conducted extensive laboratory experiments with six breeds of dog (basenjis, beagles, cocker spaniels, Shetland sheepdogs and fox terriers) using tests to measure traits such as emotional

reactivity, trainability, and problem solving. Tests of emotional reactivity included having experimenters either approach a dog speaking softly or grabbing its muzzle and shaking it from side to side. Measures of emotional reactivity, for example, included physiological measures such as heart rate and respiratory rate, as well as behavioural signals such as vocalizations and tail wagging. Under these conditions, terriers, beagles, and basenjis were judged significantly more reactive than shelties or cocker spaniels. Tests of trainability included leash training, as well as asking the dog to stand and then immediately asking it to lie down upon command. In these tests, cocker spaniels were the easiest to train, and beagles and basenjis were the most difficult. Shetland sheepdogs and terriers tended to vary on these tasks.

Scott and Fuller's (1965) studies demonstrated the value of studying behavioral traits in a laboratory study, as rarely can members of different breeds be raised in a uniform environment with the same early experience. They were also among the first to raise questions about the complexity of understanding what might constitute canine personality. Any individual with practical experience training dogs would likely guess that out of the breeds tested, the beagles and basenjis would be the most difficult to train. Beagles are a scent hound breed, easily distracted by their noses during training, while basenjis are an ancient breed, known for their independent and "cat-like" nature. These observations raise a question as to what exactly constitutes canine personality—is personality different from temperament? And when considering personality in dogs, is there a difference between behaviours at the level of the individual dog, versus traits which are inherent to a given breed?

More recent attempts at understanding differences in canine personality have been made using various methodologies, ranging from behavioral assessments (Wilsson & Sundgren, 1997; Svartberg & Forkman, 2002) to questionnaire-based studies of dog owners (Goodloe & Borchelt, 1998; Hsu & Serpell, 2003). The results have been mixed and no consensus has been reached regarding the content and number of canine personality dimensions. In an attempt to amalgamate existing literature, Jones and Gosling (2005) identified seven broad categories for ordering canine personality. They labeled these categories reactivity, fearfulness, activity, sociability, responsiveness to training, submissiveness, and aggression. It was noted by these authors, however, that existing information is limited by an over-reliance on particular populations of dogs, particularly guide dogs, police dogs or dogs trained for competition, where heterogeneity of personality traits and breed may be restricted. Another limitation is that researchers tend to focus on identifying or measuring a specific aspect of personality, such as aggression or fearfulness, rather than examining canine personality as a whole.

Recently, Stone, McGreevy, Starling, and Forkman, (2016) found associations between domestic-dog morphology and behaviour scores in the Dog Mentality Assessment (DMA). The DMA is a standardized behavioural test which was developed mainly as a tool for the selection of breeding stock in working dogs. The DMA is used by the Swedish Working Dog Association (SWDA) to test behavioural reactions of dogs to standardized stimuli and has also been used in empirical studies of personality in the domestic dog (Svartberg & Forkman, 2002). The DMA was initially used only for working breeds but is now used with other breeds and is considered a broad behavioural assessment (Saetre et al., 2006). Phenotypic measurements were recorded in the Stone et al. (2016) study from a range

of common dog breeds and included cephalic index (CI: the ratio of skull width to skull length), bodyweight, height and sex. These data were then correlated with results from the DMA, which involves trained observers scoring a dog's reaction to stimuli presented over 10 standardized subtests. Each subtest is designed to evoke a behavioural response.

Results of the Stone et al. (2016) study showed that shorter dogs demonstrated more aggressive tendencies, reacting defensively toward both assistants dressed as ghosts, as well as to a dummy. Taller dogs, on the other hand, were more affectionate when greeting and being handled by humans. Taller dogs were also more cooperative and playful with humans than shorter dogs. Heavier dogs were more inquisitive toward a dummy, to the source of a metallic noise, and to an assistant. Heavier dogs were also more attentive to assistants dressed unusually (in ghost costumes). In comparison, lighter dogs were cautious of a dummy and fearful of the sound of a gunshot. Lighter dogs were also cautious of, and demonstrated prolonged fearfulness toward, the source of a metallic noise. It was also found that CI predicted some differences in temperament. Brachycephalic dogs in this study were found to be more engaged with their owners and had a higher interest in human-directed play. These dogs were also more defensive when faced with a difficult-to-interpret situation (such as seeing a person dressed like a ghost). The dolichocephalic dogs were less likely to engage in object play, especially with unfamiliar humans. These dogs, however, were not as easily startled and recovered more quickly when an unexpected event occurred.

One of the most well established inventories of canine personality to date is the Canine Behavioral Assessment and Research Questionnaire (C-BARQ; Hsu & Serpell, 2003). The C-BARQ was designed by researchers at the University of Pennsylvania to provide dog owners and professionals with standardized evaluations of canine temperament

and behavior. It is one of the only measures of canine personality to have been extensively tested for reliability and validity on large samples of dogs from 30 different breeds (Duffy, Hsu, & Serpell, 2008). In developing the C-BARQ, owners were asked to complete a questionnaire consisting of 152 items eliciting information on how dogs responded to specific events and situations in their usual environment. Data from completed questionnaires were subjected to factor analysis, and the resulting factors were tested for reliability and validity. Factor analysis yielded 11 factors (stranger-directed aggression, owner-directed aggression, stranger-directed fear, nonsocial fear, dog-directed fear or aggression, separation-related behavior, attachment or attention-seeking behavior, trainability, chasing, excitability, pain sensitivity). The C-BARQ has become one of the dominant assessments of canine behaviour and has proved useful in screening dogs for temperament problems and in evaluating the clinical effects of various treatments for behavior problems.

One limitation of the C-BARQ is that is does not cover the full spectrum of canine personality and behaviour, focusing instead on items related to fear and aggression. The Monash Canine Personality Questionnaire (MCPQ), in contrast, explores the structure of canine personality using an adjective-based method previously used to characterize human personality (Digman, 1996). A list of 67 words was rated by 1016 dog owners for their applicability to their dog. PCA revealed five components underlying canine personality, best represented by just 41 words. Principal component analysis revealed five underlying factors that accounted for 32.6% of the total variance. Two of these, extraversion (8.3% of variance) and neuroticism (4.6%), are similar, but not identical, to dimensions identified in other species. The remaining three, tentatively labeled self-assuredness/motivation (6.5%), training focus (6.7%) and amicability (6.4%), may be unique to canines and reflective of the strong

and unique selective pressures exerted on this species by humans (Ley, Bennett & Colman 2009). The results of this study are of practical importance in that, following further validation studies, the final 41 words may be of use to rapidly assess and describe personality in individual adult dogs, and draw on a broader range of behaviours than most other measures. Furthermore, the identification of five underlying personality components is also important theoretically, helping to understand the structure of canine personality, much as the identification of the "big five" or OCEAN (openness, conscientiousness, extraversion, agreeableness, and neuroticisim) traits (Goldberg, 1990) has contributed to understanding of human personality.

Individual differences in subjects are a possible concern when studying domestic dogs—differences in breed, training, and personality may all make the study of more basic cognitive abilities difficult, if dogs react or co-operate differently in an experimental procedure. Studies of dog personality have shown that personality concepts can be applied to dogs but also suggest that canine personalities may not fall into the same dimensions as do human personalities. Understanding differences in canine personality and developing reliable ways of measuring them clearly have a practical application in the dog training realm. These same tools may also be useful in a research context, however, as behavioural scores could be correlated with performance on cognitive tasks to determine what, if any, effects individual differences among subjects may have in cognitive studies of dogs.

This extensive inventory of individual differences in dogs underscores what is arguably the biggest limitation of the presented studies—small sample sizes. Given the high number of sessions and trials needed to run these studies, it became logistically difficult to find subjects who could complete these tasks in full. Future studies will take this into

consideration, and attempt to design procedures that will allow for higher N values. This said, small sample sizes are commonly accepted (albeit not ideal) in species in which it difficult or impossible to obtain a large sample size (i.e. chimpanzees and other non-human great apes); small sample sizes in these cases are absolutely a limitation, but by no means make such research inconsequential. It could also be argued that when it comes to fundamental cognitive traits, one should not expect to see overwhelming variability in subjects who are all members of the same species. Furthermore, the goal of these studies was not to determine the average performance of dogs on said tasks, but rather to establish whether or not the species in question has these capabilities at all. As much as the author would like to believe that Sedona is singularly unique in her ability to discriminate number (the author also being Sedona's doting owner), it is unlikely that she alone possesses these skills amongst her canine brethren.

fMRI Studies: A Viable Tool in the Study of Dog Cognition?

A rapidly emerging area of study involves functional magnetic resonance imaging (fMRI) of the domestic dog. Explorations in dog MRI and fMRI began with the use of sedation in order to study anatomy and physiology of the dog—these studies were conducted primarily for veterinary education and research. FMRI makes use of the flow of oxygenated blood as a correlate of neural activity in particular brain regions during a task. When neurons in the brain are activated during a given activity, an increased volume of oxygenated blood flows to the region in which these neurons are located in order to meet their energy demands. Given many repetitions of a thought, action or experience, statistical methods can be used to determine what areas of the brain are active during that thought or action. One major benefit

of working with dogs (as opposed to other non-human animals) is that the trainability of dogs allows for neuroimaging to be conducted noninvasively in an awake and unrestrained state.

A major practical consideration in working with any type of non-human animal is how to keep the subject still in the fMRI--even the slightest motion can result in physiological noise in the resulting scan, which is an expensive process. Researchers have used a variety of techniques to train dogs for fMRI, including the use of target sticks (Jia, Pustovyy, Waggoner, et al., 2014), chaining (Berns, Brooks, & Spivak, 2013) and model-rival techniques (Andics, Gácsi, Faragó, Kis, & Miklósi, 2014). Training techniques typically involve conditioning the dog to rest its chin on a mock apparatus, and eventually moving the dog into a real scanner. Given the expense of fMRI research, a practical consideration is the development of training techniques which promote rapid acquisition of behaviours required for scanning, while imposing minimum stress upon the animal.

Berns, Brooks and Spivak (2012) were the first to publish an fMRI study using awake, unrestrained dogs. They followed up this study with an assessment of the replicability of their method (Berns, Brooks, & Spivak, 2013). The primary purpose of the Berns et al. studies was to successfully demonstrate a usable methodology for studying dogs unrestrained in a scanner. A simple task was therefore used—in one condition, a handler held his or her hand straight up in front of the dog, and a reward followed. In the second condition, the handler held both hands horizontally facing each other, which signaled no reward. Results of both studies found that when dogs were given the signal predicting reward, increased activation was found in the caudate nucleus, which among other things is considered the "reward centre" of the brain.

Temperament issues may also be explored in the context of FMRI studies. Cook, Spivak and Berns (2014) had owners complete the self-reported Canine Behavioural Assessment and Research Questionnaire (C-BARQ). Results of this study found that dogs with lower levels of aggression showed greater activation for reward signals when these signals were given by a familiar person than when they were given by a stranger or computer. Dogs demonstrating higher aggression, on the other hand, showed greater activation when reward signals were given by the stranger or a computer. Cook et al. note that these results are likely explained by the fact that striatal response is based upon arousal and stimulus salience. Higher aggressiveness correlates with higher salience for the novel human or computer, while lower aggression correlates with lower anxiety and higher salience with a familiar person. Differences in dog temperament may be a double-edged sword. On the one hand, they may be a source of quality research questions which can be addressed through fMRI. On the other hand, they are a source of individual variation which must be carefully considered in order to avoid confounding studies.

Since the introduction of fMRI as a technique for working with dogs, studies have emerged on a broader range of topics related to dog cognition. Andics et al. (2014) compared voice-sensitivity in both dogs and humans by having all subjects listen to the same set of stimuli, which included both dog and human vocalizations. Cortical activation was found primarily in the perisylvian region for dogs, and in the superior temporal sulcus and inferior frontal cortex for humans. In dogs, maximum activation was found for dog vocalizations, as well and human vocalizations and environmental sounds. In humans on the other hand, nearly all areas of activation showed maximal activation for human vocalizations. These differences in activation likely reflect the importance of attending to humans in canines.

Jia, Pustovyy, Waggoner, et al. (2014) compared neural responses in the brain to different odor concentrations in awake vs. anesthetized dogs. Dogs were presented with 10-s periods of ethyl butyrate, eugenol, or carvone mixture in either low or high concentrations. Both awake and anesthetized dogs demonstrated strong activation in the olfactory lobe and bilateral piriform lobes for both low and high concentration of odors. Awake dogs (but not anesthetized dogs) also exhibited activation in the frontal cortex and cerebellum—both of which are associated with cognitive processing. Given these findings, the authors concluded that the use of anesthetic degrades the processing of odors, making the use of awake and unrestrained dogs an important advancement in using fMRI to study the olfactory system.

Dilks et al. (2015) were the first to publish an fMRI study of face processing in dogs. Dogs were presented with both movie clips and static images in this study. Movie clips of human faces, scenes, objects and scrambled objects were all presented for 3 s each. Static black and white images of human faces, dog faces, objects, scenes, and scrambled faces were presented for 600 ms each. Activation was found for movie clips of both dog and human faces in the inferior temporal cortex in the right hemisphere. Additionally, more activation was found for static images of faces compared to static images of objects and scenes. Dilks et al. (2015) concluded that these findings suggest the existence of a face-processing region in dogs.

Practical considerations in the use of fMRI with dogs include procedural issues (can dogs really be kept still long enough to obtain a clean scan) as well as monetary concerns—it is extremely expensive to conduct fMRI research. Are questions concerning dog cognition worthy of such expenditures, when there are plenty of more developed areas of research in fMRI to which these resources could be allocated? The work of Berns, Brooks, and Spivak

(2012, 2013) was the first to successfully demonstrate that dogs can in fact be trained to sit in a scanner unanesthetized and unrestrained. It should be noted, however, that to date, most of the studies using dogs in scanners have involved very simple procedures (ex: having the dog observe a simple hand signal). Given that the dog is already attending to an operantly trained command while in the scanner, one must wonder what, if any, activation in the scanner is related to the dog focusing on sitting still. That is, does the fact that the dog is already attending to a command (and inhibiting any movement) compromise or in any way alter activation patterns when they are subsequently given the task of interest in the scanner. Nevertheless, fMRI has proven to be a useful tool in the understanding of the canine brain and may be particularly useful when paired with data from either canine personality inventories (ex: C-BARQ) or more traditional behavioural studies.

Conclusion

Dog cognition is currently seeing its heyday in psychological research, with the bulk of studies in this area dedicated to aspects of social cognition. There remain, however, comparatively few studies examining fundamental aspects of cognition in dogs. The processing of number, time and space, for example, are crucial elements of cognition, which help an animal to survive in its day-to-day life. Although these are processes which have been studied for decades in rats, pigeons, monkeys, and other more "typical" lab species, very little on these topics have been published with respect to the domestic dog. To have a full understanding of canine cognition, an understanding of these basic cognitive processes is required. The preceding chapters a.) developed procedures and apparatus for the study of numerical discrimination, interval timing, and spatial memory in dogs, and b.) determined whether or not dogs displayed proficiency in these tasks similar to other previously tested

species. It is hoped that these chapters may contribute to further and more thorough

understanding of basic cognitive processing in the domestic dog.

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Appendix A—Ethics

Western

2009-074::7:
AUP Number: 2009-074
AUP Title: Studies in Dog Cognition

Yearly Renewal Date: 08/01/2016
The YEARLY RENEWAL to Animal Use Protocol (AUP) 2009-074 has been approved, and will be approved for one year following the above review date.

1. This AUP number must be indicated when ordering animals for this project.
2. Animals for other projects may not be ordered under this AUP number.
3. Purchases of animals other than through this system must be cleared through the ACVS office.
   Health certificates will be required.

REQUIREMENTS/COMMENTS
Please ensure that individual(s) performing procedures on live animals, as described in this protocol, are familiar with the contents of this document.
The holder of this Animal Use Protocol is responsible to ensure that all associated safety components (biosafety, radiation safety, general laboratory safety) comply with institutional safety standards and have received all necessary approvals. Please consult directly with your institutional safety officers.
Submitted by: Schoelier, Marianne
on behalf of the Animal Use Subcommittee

Appendix B—Copyright

AMERICAN PSYCHOLOGICAL ASSOCIATION LICENSE
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Dec 20, 2017

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CURRICULUM VITAE

EDUCATION

2018 (expected), Ph.D., Psychology
The University of Western Ontario
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2008 M.Sc., Psychology
The University of Western Ontario
London, Ontario, Canada

2005 B.Sc. (Hon.), Psychology
The University of Western Ontario
London, Ontario, Canada

SCHOLARSHIPS AND AWARDS

Keith Humphrey Memorial Award (2014)
Western Graduate Research Scholarship (2013)
Western Graduate Research Scholarship (2012)
Sonny Tougas Award (2011)
Queen Elizabeth II Graduate Scholarship in Science/Technology (2011)
Western Graduate Research Scholarship (2011)
Western Graduate Research Scholarship (2010)
Western Graduate Research Scholarship (2007)
Reva Gerstein Award (2006)--$2700.00
Western Graduate Research Scholarship (2006)
McClelland Award (2005)
Canadian Federation of University Women Award (2000)

TEACHING EXPERIENCE

Course Instructor
- Introduction to Animal Cognition (Winter 2018)
- Introduction to Research Methods (Winter 2017)
- Introduction to Animal Cognition (Winter 2016)
- Introduction to Animal Cognition (Winter 2015)

Teaching Assistantships
- Lab Coordinator, Introduction to Research Methods (2012, 2013)
- Section TA, Introduction to Research Methods (2006, 2007, 2010, 2011)

RESEARCH EXPERIENCE

- Research Assistant (2006-2008, 2010-present)
  Western University
  Supervisor: William A. Roberts, Ph.D.

PUBLISHED PEER-REVIEWED JOURNAL ARTICLES

Macpherson, K., & Roberts W.A. (2017). On the clock: Interval timing and overshadowing in domestic dogs (*Canis familiaris*). *Journal of Comparative Psychology, 131,* 348-361.

Roberts, W.A., MacDonald, H., Brown, L., & Macpherson, K. (2017). Release from proactive interference in rat spatial working memory. *Learning & Behavior, 45,* 263-275.

Roberts, W.A., & Macpherson, K. (2016). Of dogs and men. *Current Directions in Psychological Science*, *25*, 313-321.

Roberts, W.A., Macpherson, K., & Strang, C. (2016). Context controls access to working and reference memory in the pigeon (*Columba livia*). *Journal of the Experimental Analysis of Behavior, 105, 184-193.*

Roberts, W.A., Strang, C. & Macpherson, K. (2015). Memory systems interaction in the pigeon: Working and reference memory. *Journal of Experimental Psychology: Animal Learning and Cognition, 41, 152-162.*

Macpherson, K., & Roberts, W.A. (2013). Can dogs Count? *Learning & Motivation, 44*, 241-251.

Roberts, W.A., & Macpherson, K. (2011). Theory of mind in dogs: Is the perspective-taking task a good test? *Learning & Behavior, 39,* 303-305.

Macpherson, K., & Roberts, W.A. (2010). Spatial memory in dogs (*Canis familiaris*) on a radial maze. *Journal of Comparative Psychology, 124,* 47-56.

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Roberts, W.A., Feeney, M.C., McMillan, N., Macpherson, K., Musolino, E., & Petter, M. (2009). Do pigeons (Columba livia) study for a test? *Journal of Experimental Psychology: Animal Behavior Processes, 35,* 129-142.

Roberts, W.A., Feeney, M.C., Macpherson, K., Petter, M., McMillan, N., & Musolino, E. (2008). Episodic-Like Memory in Rats—Is it Based on When or How Long Ago? *Science, 320,* 113-115.

Macpherson, K., & Roberts, W.A. (2006). Do dogs (*Canis familiaris*) seek help in an emergency? *Journal of Comparative Psychology, 120,* 113-119.

CONFERENCE POSTERS (Presenting author is underlined)

Macpherson, K., & Roberts, W.A. (2012). *Can Canines Count?* Poster presented at the 3rd bi-annual meeting of the Canine Science Forum, Barcelona, Spain.

McMahon, S., Macpherson, K., & Roberts, W.A. (2010, October). *Dogs choose a human informant: Metacognition in canines.* Poster presented at the 17th annual meeting of the Association of Pet Dog Trainers, Atlanta, GA.

McMahon, S., Macpherson, K., & Roberts, W.A. (2010, July). *Dogs choose a human informant: Metacognition in canines.* Poster presented at the 2nd bi-annual meeting of the Canine Science Forum, Vienna, Austria.

Macpherson, K., & Roberts, W.A. (2008, June). *Spatial memory in domestic dogs (Canis familiaris).* Poster presented at the 18th annual meeting of the Canadian Society for Brain, Behaviour, & Cognitive Science, London, ON, CA.

Roberts, W.A., Feeney, M.C., Macpherson, K., Petter, M., McMillan, N., & Musolino, E. (2008, March). *Episodic-like memory in rats—Is it based on when or how long ago?* Poster presented at the 15th annual meeting of the Society for Comparative Cognition, Melbourne Beach, FL.

Macpherson, K., & Roberts, W.A. (2008, March). *Studies of spatial memory in domestic dogs using a radial maze.* Poster presented at the 15th annual meeting of the Society for Comparative Cognition, Melbourne Beach, FL.

Macpherson, K., & Roberts, W.A. (2007, March). *Some studies of spatial memory in domestic dogs.* Poster presented at the 14th annual meeting of the Society for Comparative Cognition, Melbourne Beach, FL.

CONFERENCE TALKS (Presenting author is underlined)

Macpherson, K., Lo, K.H. & Roberts, W.A. (2018, March). *Olfactory memory capacity and duration in domestic dogs..* Talk given at the 25th annual meeting of the Society for Comparative Cognition, Melbourne Beach, FL.

Macpherson, K., & Roberts, W.A. (2016, March). *Reference and working memory in the domestic dog using a spatial memory task.* Talk given at the 23rd annual meeting of the Society for Comparative Cognition, Melbourne Beach, FL.

Roberts, W.A., Strang, C.G., & Macpherson, K. (2016, March). *Context and memory in the pigeon.* Talk given at the 23rd annual meeting of the Society for Comparative Cognition, Melbourne Beach, FL.

Macpherson, K., & Roberts, W.A. (2015, March). *Interval timing and overshadowing in domestic dogs.* Talk given at the 22nd annual meeting of the Society for Comparative Cognition, Melbourne Beach, FL.

Macpherson, K., & Roberts, W.A. (2014, July). *Interval timing in domestic dogs.* Talk given at the 24th annual meeting of the Canadian Society for Brain, Behaviour, and Cognitive Science, Toronto, ON.

Macpherson, K., & Roberts, W.A. (2014, June). *Can dogs count?* Talk given at the 2nd annual meeting of the Society for the Promotion of Applied Research in Canine Science, Newport, RI.

Roberts, W.A., Strang, C.G., & Macpherson, K. (2014, March). *The interaction of working and reference memory in pigeons.* Talk given at the 21st annual meeting of the Society for Comparative Cognition, Melbourne Beach, FL.

Macpherson, K., & Roberts, W.A. (2014, March). *Interval timing in the domestic dog.* Talk given at the 21st annual meeting of the Society for Comparative Cognition, Melbourne Beach, FL.

Macpherson, K., & Roberts, W.A. (2013, November). Can dogs discriminate time and number? In Roberts, W.A., (Chair), *Exploring the Canine Mind: Studies of Dog Cognition.* Symposium conducted at the 54th annual meeting of the Psychonomic Society, Toronto, ON.

Macpherson, K., & Roberts, W.A. (2013, November). *Reference and working memory in a spatial memory task with domestic dogs.* Talk given at the 6th annual fall meeting of the Comparative Cognition Society, Toronto, ON.

Macpherson, K., & Roberts, W.A. (2013, May). *Counting, timing, and the domestic dog.* Talk given at the Ontario Ecology, Ethology, and Evolution Colloquium, London, ON.

Macpherson, K., & Roberts, W.A. (2013, March). *Studies of interval timing and numerical discrimination in the domestic dog.* Talk given at the 20th annual meeting of the Comparative Cognition Society, Melbourne Beach, FL.

Macpherson, K., & Roberts, W.A. (2012, October). *Can canines count?* Talk given at the 19th annual meeting of the Association of Pet Dog Trainers, Covington, KY.

Roberts, W.A., McMillan, N. & Macpherson, K. (2011, March). *Rats respond for information in a T-Maze.* Talk given at the 18th annual meeting of the Society for Comparative Cognition, Melbourne Beach, FL

Macpherson, K., & Roberts, W.A. (2011, March). *Numerical discrimination in domestic dogs.* Talk given at the 18th annual meeting of the Society for Comparative Cognition, Melbourne Beach, FL.

COLLOQUIA AND INVITED TALKS (Presenting author is underlined)

Macpherson, K. (2015, October). *Time, space, number…and the domestic dog.* Western University Senior Alumni Speaker Series, London, ON.

Macpherson, K. (2014, October). *Dog cognition: Studying the minds of our canine companions.* London Pet Show & Purina National Dog Show, London, ON.

Macpherson, K. (2014, May). *Inside the mind of the domestic dog.* London Guest speaker series, London North Rotary Club, London, ON.

Macpherson, K. (2014, February). *Domestic darlings—Dogs in animal cognition Research.* E-Training for Dogs. Online Lecture.

Macpherson, K. (2012, November). *Dog science! Understanding the cognitive world of our canine companions.* Speaker Series, Winter Woofstock, Toronto, ON.

Macpherson, K. (2012, February). *Domestic dogs: The new darlings of animal cognition.* Psychology colloquia talk, University of Windsor, Windsor, ON.

Macpherson, K., & Roberts, W.A. (2011, June). Anthropomorphism and the domestic dog. In D. Kelley (Chair), *Comparative cognition: The next generation.* Symposium conducted at the 21st annual meeting of the Canadian Society for Brain, Behaviour, & Cognitive Science, Winnipeg, MB.

Roberts, W.A., & Macpherson, K. (2009, May). *Are dogs really man's best friend?* London Public Library psychology speaker series, London, ON.

SCIENTIFIC SERVICE

Committees
- Western Psychology Department Colloquia Series, Organizing Committee, 2014-2015.
- Ontario Ecology, Ethology, and Evolution Colloquium (OE3C). Organizing Committee, 2013.
- Graduate Student Representative, Space and Facilities Committee (2008, 2009).

Peer Review
- Animal Behaviour
- Animal Cognition
- Learning & Motivation
- Personality & Individual Differences