8-12-2020 10:00 AM

The olfactory and auditory capabilities of dogs (Canis lupus familiaris) for locating different quantities of food

Shayla Jackson, *The University of Western Ontario*

Supervisor: Roberts, William, *The University of Western Ontario*
Co-Supervisor: Sutton, Jennifer, *The University of Western Ontario*
A thesis submitted in partial fulfillment of the requirements for the Master of Science degree in Psychology

Abstract

Although some animals, such as elephants, can use olfaction to discriminate quantities of food, previous research suggested dogs cannot smell the difference between quantities of hot dog slices. In the experiments reported here, dogs were allowed to smell two opaque containers under which were placed different numbers of hot dog slices, and then were allowed to make a choice between containers. In Experiment 1, dogs chose between one and five hot dog slices and chose the larger quantity at an above chance level. In Experiment 2 and Experiment 3, I tested whether dogs conformed to the distance effect and/or the ratio effect when smelling quantities and found no evidence of either effect. In a fourth experiment, I tested whether the type of food used influenced the performance of dogs and found that the performance of dogs was higher when hot dog slices were used as reinforcement rather than kibble pieces. In the fifth experiment, I tested whether dogs could hear the difference between quantities of hot dog slices and found no evidence of quantity discrimination in this modality. These results suggest that dogs are capable of using olfaction to discriminate quantities of food based on amount, but not number, of hot dog slices.

Keywords

Olfaction, Dog, Canine, Cognition, Auditory, Numerosity Effects, Distance Effect, Ratio Effect, Quantity, Food Type

Summary for Lay Audience

I wanted to replicate an experiment in which it was found that dogs could not locate a larger quantity of hot dog slices by scent when visual information was hidden. When I replicated this study with more trials per dog, I found that dogs were able to find the larger quantity above chance level. In my second experiment, I tested if dogs were better at discriminating quantities that were farther apart in number or at lower ratios (when the small quantity is divided by the large quantity). Because I found no evidence for either effect in my second experiment, my third experiment replicated my second experiment but used wider number distances and ratio differences in order to increase the saliency of these differences. Again, I found no evidence for either effect. In my fourth experiment, I tested if dogs find the larger quantity better when certain food types are used. I found that dogs found the larger quantity more often when tested with hot dog slices as compared to kibble pieces. In my fifth experiment, I tested whether dogs could hear the difference between quantities of hot dog slices when a container was shaken. Because dogs performed above chance on the odor control condition that I used in this experiment, I could not conclude that dogs were able to discriminate quantities in this modality.

Co-Authorship Statement

All of the experiments I performed were supervised by Dr. William A. Roberts and Dr. Jennifer E. Sutton. Glynis Kathrene Martin assisted in data collection. Dr. William A. Roberts and Glynis Kathrene Martin will be listed as co-authors for future publication.

Acknowledgments

Firstly, I would like to thank my supervisor, Bill. You have offered me invaluable advice on countless occasions throughout my undergraduate work and into my pursuit of my master's degree. Most of my research skills in experimental design, execution, and write-up I have learned from you. I will be forever grateful for how you have shaped my development as a researcher.

I would also like to extend this thanks to everyone else on my supervisory committee: Dr. Jennifer Sutton, Dr. Scott MacDougall-Shackleton, and Dr. Graham Thompson. Your diverse views of animal cognition have broadened the scope of my thesis. You have all been exemplary role models to me in my professional development and I thank you for that.

Secondly, I would like to thank Glynis. You have helped test many dogs in many projects. In addition to being an excellent mentor to me in the running of the lab, you have also been an excellent friend. Our lab could not run as smoothly as it has without you, or our excellent volunteers who give up their time for the pursuit of understanding animal cognition.

This gratitude must also be extended, to Gordon Lo. Even after your departure from our lab, you have reached out on several occasions to assist me with various projects. Your advice, mentorship and friendship have helped me many times.

I would also like to thank the dog owners, as well as the dogs that participated in this set of experiments. Without you, none of this would be possible.

Finally, I would like to thank my family for standing with me through the ups and downs of my academic pursuit. Your support has kept me going at the most frustrating of times, and I truly could not have reached the point I am at without you.

Table of Contents

List of Tables

List of Figures

List of Appendices

Chapter 1

1 Introduction

1.1.1 The Olfactory Capabilities of Dogs

Dogs (*Canis lupus familiaris*) have an excellent sense of smell, which has been well-documented by researchers throughout the years. Kalmus (1955) showed that dogs are able to detect the olfactory difference between twins, and King, Becker, and Markee (1964) showed that dogs are capable of detecting undisturbed scents that are well over a month old. Expanding this work, Lo, Macpherson, MacDonald, and Roberts (2020) showed that dogs are capable of discriminating over 20 different essential oil scents and remembering these discriminations for upward of a month. Dogs can even use the information they gather about scents to form episodic-like memories (Lo & Roberts, 2019). More recently, Krichbaum, Rogers, Cox, Waggoner, and Katz (2020) showed that in an odour span task in which dogs were rewarded for choosing new scents, dogs were able to remember 72 different scents within a session, even when the familiar scent had been presented several trials ago, indicating excellent olfactory working memory ability. Dogs are able to detect scents that humans cannot because of their greater number of active genes devoted to detecting scents. Both dogs and humans have about 1000 genes responsible for scent detection (Zozulya, Echeverri, & Nguyen, 2001), but about 70% of these genes are deactivated in humans (Rouquier et al., 1998), whereas only about 20% are deactivated in dogs (Quignon et al., 2005), meaning dogs are able to detect odours that humans cannot, even when strong.

Dogs, and other mammals, detect these odours when molecules are inhaled to the nasal cavity, causing the activation of olfactory receptors (Quignon et al., 2005). These receptors send signals of their detection of a scent to the olfactory bulb in the brain, which then sends them to other cognitive areas of the brain (Malnic, Hirono, Sato, & Buck, 1999), such as the pyriform cortex, entorhinal cortex and orbitofrontal cortex. These areas of the cortex are involved in odour discrimination, spatial memory and decision-making, respectively (Gadbois & Reeve, 2014).

Aside from dogs' sense of smell being useful to humans (Steen, Mohus, Kvesetberg, & Walløe,1996; Gazit & Terkel, 2003; Hackner & Pleil, 2017), it is also beneficial for dogs. Duranton and Horowitz (2019) gave dogs a cognitive bias test before and after extensive practice in either scent detection or a control activity and found that dogs that had been engaged in scent detection were more likely to approach an ambiguous stimulus, specifically a pot, than those that had practiced the control activity, showing that scent detection can encourage a positive judgement bias in dogs. Overall and Dyer (2005) recommend olfactory stimulation as a source of enrichment for dogs, and this type of enrichment can be used to calm rescue dogs in their kennels (Graham, Wells, & Hepper, 2005). Other types of enrichment have been used to improve performance on a cognitive task in older dogs that have experienced cognitive decline with age (Milgram, 2003). From a neurobiological perspective, a greater amount of brain-derived neurotrophic factor is thought to be involved in a greater cognitive performance, and this amount can be increased through enrichment (Fahnestock et al., 2012). Through comparing the performance of different groups of dog breeds, Polgár, Kinnunen, Újváry, Miklósi, and Gácsi (2016) showed that although scent-bred dogs are superior to other breed groups in a scent detection task, all dogs were able to detect the scents at an above chance level at all but the hardest levels of detection, suggesting this benefit of olfactory stimulation might be obtained by all dogs, regardless of breed.

1.1.2 Animals Discriminating Quantities via Olfaction

Given the rich literature on dogs' olfactory capabilities, it is surprising that although several researchers have shown that dogs can smell stronger scents better than weaker scents (King et al., 1964; Cablk, Sagebiel, Heaton, & Valentin, 2008) not much work has been done on their ability to smell differences in quantity. In a single-trial test, Horowitz, Hecht, and Dedrick (2013) gave dogs a choice between 1 and 5 hot dog slices. Both quantities were hidden inside folded paper plates. Surprisingly, although dogs paid more attention to the larger quantity during their initial investigation, this apparent preference was not reflected in the choice phase; that is, dogs did not show a significant preference for the larger quantity when choosing between the quantities.

Similar work has been done with elephants (*Elephas maximus*). Plotnik et al. (2019) gave elephants several choices between a large quantity and a small quantity. The researchers used 11 different ratios of quantities that ranged from 4-24g of sunflower seeds. In each trial, both quantities were hidden inside lidded plastic buckets. Unlike the dogs, the elephants performed very well on this task. Their performance increased with low ratio discriminations (ex. 1:2 lower than 5:6) and greater distance between the quantities but showed no change dependent on the overall magnitude of the food presented.

1.1.3 Animals Discriminating Quantities via Audition

As for the auditory modality, although there has been plenty of work showing animals' ability to follow auditory direction to food, such as in the work of Hare et al. (2002) with dogs and wolves, there has been a comparably minimal amount of controlled research done on animals' abilities to hear quantity.

Mammals detect sound when sound waves pass through the ear canal, through the ear drum and middle ear structures to the inner ear. These vibrations cause the fluid within the cochlea of the inner ear to move, which then result in hair cells known as auditory receptors to move. These auditory receptors function as an all-or-none response system and send the signal that sound has been detected to the central nervous system through the auditory nerve (Weiss, 1966). In the canine brain, auditory stimuli activate the medial geniculate nucleus and caudal colliculus of the auditory pathway, but unlike in humans, there is little response to auditory stimuli in the temporal cortex (Bach et al., 2013). These areas of the brain are thought to be involved in emotional responses to auditory stimuli (LeDoux, Sakaguchi, & Reis, 1984;), orienting movements (Sahibzada, Dean, & Redgrave, 1986) and mental representations (Haxby, Gobbini, Furey, Ishai, Schouten, & Pietrini, 2001), respectively.

Beran (2012) tested three chimpanzees (*Pan troglodytes*) on their ability to locate the larger quantity of food via auditory cues. Each chimpanzee was presented with two containers; both of which had a number of food items dropped into it sequentially that the chimpanzee could hear but not see. All three chimpanzees were able to locate the larger amount at above-chance levels, and they performed better on quantities that were farther apart in space and on lower ratio discriminations.

Similar auditory discrimination work has also been done in elephants. Plotnik, Shaw, Brubaker, Tiller, and Clayton (2014) tested seven elephants on their ability to hear differences in quantity by offering a choice between two containers, only one of which contained food. Prior to allowing the elephants to choose a container, each container was shaken. Since only one of the containers had food inside, only one of the containers made noise when shaken. Unlike the chimpanzees, the elephants were not able to locate the larger food quantity based on auditory cues at an above-chance level.

Benson-Amram, Gilfillan and McComb's (2017) review of the literature on numerical assessment in animals reveals that in the wild, auditory assessments of quantity are quite common. Lions (*Panthera leo*) and hyenas (*Crocuta crocuta*) are sensitive to the number of conspecific calls in playback experiments, investigating the sounds of intruders more quickly when fewer intruder calls are played. Hyenas discriminated sequentially presented calls of both known and unknown individuals, requiring discrimination between individual callers. Wolves (*Canis lupus*) are more likely to return human-made howls when they are in a larger group, and even barn owls (*Tyto alba*) are sensitive to the number of conspecifics based on playback calls. However, these field studies lack the control of testing done on captive or domesticated animals.

In dogs, Bräuer, Kaminski, Riedel, Call, and Tomasello (2006) found that dogs were able to locate a hidden quantity of food more reliably when auditory cues were provided. Dogs were given a choice between two containers, only one of which contained food. Dogs reliably located the food when only the container with food was shaken but reliably failed to find the food when only the container without food was shaken, suggesting they had learned only to approach the container that made a sound when shaken. A condition in which both containers were shaken was not included. Therefore, dogs' ability to locate a larger quantity of food based on auditory information from both containers is not clear from this experiment.

1.1.4 Animals Discriminating Quantities via Vision

In contrast to the small amount of research on animals' olfactory and auditory numerical discrimination abilities, there has been a large literature on animals' visual numerical discrimination abilities, including such species as chimpanzees (Boysen & Berntson, 1989), tortoises (*Testudo hermanni*; Gazzola, Vallortigara, & Pellitteri-Rosa, 2018) and honeybees (*Apis mellifera* L.,; Dacke & Srinivasan, 2008). When dogs are presented with a choice between a large quantity and a small quantity that they can see, they reliably choose the larger quantity, even when this visual information is not available at the time of choice (Ward & Smuts, 2007). Recent work has shown that the ability to discriminate visual quantities is fairly developed even at 2 months of age (Petrazzini, Mantese, & Prato-Previde, 2020). In adult dogs, visual quantity discrimination appears to be more complex. Adult dogs perform better on quantities that are farther apart (Ward & Smuts, 2007) and on lower ratio discriminations when dealing with either food (Petrazzini & Wynne, 2016) or non-food (Macpherson & Roberts, 2013) items.

Other animals have also shown these effects. Dehaene, Dehaene-Lambertz, and Cohen (1998) note that many of the numerical discrimination strategies of humans are also present in many animals. Two commonly discussed effects are the distance effect and the ratio effect. The distance effect predicts that quantities with a greater distance between them will be easier to discriminate than quantities with a lesser distance between them. The ratio effect predicts that quantities with a greater ratio (when the small quantity is divided by the large quantity) will be harder to discriminate than quantities with a lesser ratio. In addition to dogs (Ward & Smuts, 2007; Petrazzini & Wynne, 2016; Macpherson & Roberts, 2013), both of these effects have been found in chimps (Beran, 2001) and pigeons (*Columba livia domestica*; Roberts, 2010) when dealing with visual quantities. These numerosity effects, particularly the ratio effect, can be seen as indicative of an approximate number system (Brannon & Merritt, 2011), which portrays quantities as approximate values on an internal number line, making quantities that are farther apart easier to discriminate than quantities that are closer to one another (Piazza, 2010).

The approximate number system, and by extension the distance and ratio effects, is consistent with Weber's law, that the just noticeable difference in a stimulus' intensity will remain a constant proportion of the intensity of the original stimulus (Piazza, 2010). This is why numerical discrimination becomes less accurate at higher ratios. It also means that discrimination is limited to approximate, rather than precise (as in the symbolic number system), values (Brannon & Merritt, 2011).

1.1.5 The Effect of Food Type on Discrimination

Another factor that may affect animals' performance on a two-way object choice paradigm task is the type of food used as reinforcement. In a simple experiment, Pattison and Zentall (2014) demonstrated dogs' preference for cheese over carrot. Capaldi, Miller, and Alptekin (1989) have shown that rats (*Rattus norvegicus domestica*) are capable of using the pattern of food type used as a reward on independent trials as a cue to when non-reinforced trials will occur, indicating an ability to modify behaviour based on reward. Given that different types of rewards can lead to different levels of motivation (Loveland & Olley, 1979; Markova & Ford, 2011), one would expect animals to work harder for food items of higher value to them. In support of this view, information is sent to the orbitofrontal cortex during scent detection, which is involved in decision-making and the anticipation of rewards (Gadbois & Reeve, 2014) It could also be the case that quantitative differences are easier to detect in certain food types. For instance, food types with stronger odours may be easier to discriminate from one another by scent than food types with weaker odours.

1.2 Current Study

In the present study, I investigated the olfactory capabilities of dogs by first testing their ability to smell a small quantity of hot dog slices versus a larger quantity of hot dog slices. Following this, I investigated the numerical discrimination abilities of dogs when dealing with olfactory cues by testing their performance on a number of different ratio discriminations. The effect of differing food type was also investigated as a factor on performance when finding the larger quantity with olfaction. Finally, I investigated the auditory capabilities of dogs for discriminating between different amounts of food. This set of experiments is the first to my knowledge to extend olfaction work in dogs to numerical discrimination effects and to test the auditory capability of dogs for discriminating quantities in a two-way object choice paradigm wherein information comes from both containers. It is also the first study to consider the effect of food type in numerical discrimination when both options in a trial consist of the same food type.

Based on the previous works discussed, I hypothesized that in contrast to the findings of Horowitz et al. (2013), dogs will be able to discriminate larger quantities of hot dog slices from smaller quantities and that this performance would show the distance and ratio effects. Furthermore, I predicted that food type would have a significant effect on dogs' ability (or inclination) to locate the larger quantity. Extending this work to other modalities, I also expected that dogs would be able to discriminate larger quantities from smaller quantities of hot dog slices when receiving auditory rather than olfactory cues.

Chapter 2

2 Experiments

2.1 General Methods

In this section, I describe the general methods followed for all experiments. Variations from these general methods are presented with each experiment.

2.1.1 Subjects

Ten pet dogs of various breeds were tested in each experiment. All dogs were fasted for several hours prior to testing, and constant access to water was available during testing. Care of all the animals tested in the following experiments followed Canadian Council on Animal Care guidelines and was approved by the Western University Animal Care Committee. The demographics of the dogs used in the following experiments can be seen in Appendix A.

2.1.2 Apparatus

I used grey, plastic containers, that measured 10 cm × 16 cm with a height of 5.5 cm, to hide the location of each quantity of hot dog slices. Each container had four parallel openings that were 2 cm long in its base, to allow for air flow through the base of the container. These containers sat overturned on top of white paper plates that had a diameter of 22.5 cm. Hot dog slices were cut into 2 cm wide by 2 cm long sections and then halved into semicylinders. For smaller dogs, these semicylinders were then halved again, maintaining the semicylinder shape. A cardboard blind that measured 122 cm × 91 cm was used to prevent dogs from seeing where the experimenter placed each quantity on each trial.

2.1.3 Procedure

Each of the 10 dogs completed a number of choice trials, which they were led through by a handler. The number of trials was determined by the tolerance of the dogs for completing them.

All trials began with the dog behind a sheet of cardboard that was used as a blinder for the dog while the experimenter set up the trial. The handler held the dog behind this sheet of cardboard; both the dog and the handler were blind to the experimenter's set up of the trial. For each trial, two grey, plastic containers were set up, each overturned on top of a white paper plate. One of the plates had a smaller quantity of hot dog slices on it, and the other plate had a larger quantity of hot dog slices on it, both of which were hidden from sight by the overturned container on top of the plate. The quantity on each plate was counterbalanced so that each quantity appeared with equal frequency on each plate in a random order. Each container with its plate and hot dog slice quantity was set up an equal distance from the dog, such that the dog behind the blinder was centered between the two containers. The dog was approximately 0.5 m behind the center line of the two containers.

Once the trial was set up, the blind was removed, and the containers were revealed. The experimenter sat behind the center line of both containers, opposite the dog, with a fixed gaze set between the containers. At this point the dog was allowed to move forward toward the containers and approach whichever container it desired first. The dog was allowed to smell the container for 3 s before being directed to smell the other container for 3 s. For dogs that did not automatically smell the containers upon approach, smelling the container was encouraged by the experimenter tapping the top of the container and asking, "What's that?". No dogs refused to sniff the container after receiving encouragement. In all trials, if one container was encouraged, the other was also encouraged to prevent bias toward one container over the other. For dogs that tried to flip the containers during the investigation phase, the experimenter placed a hand on each container to hold them steady.

After both containers had been smelled, the handler pulled the dog back 0.5 m from the containers and centered the dog between the containers, such that the dog was an equal distance from each container. The dog was held in this position for another 3 s before being released by the handler. At this point, the dog approached one of the containers and removed the hot dog slices from underneath. For dogs that had trouble removing the container on their own, the chosen container was lifted, allowing easy access to the hot dog slices beneath. The unchosen container, plate and hot dog slices were removed by the experimenter. Once all the hot dog slices under the chosen container had been eaten, the handler retrieved the dog, and the experimenter set up the next trial.

2.2 Experiment 1

In the first experiment, dogs were offered a choice between a hidden quantity of 1 hot dog slice and a hidden quantity of 5 hot dog slices in order to determine if they could smell the larger quantity. All the dogs used in this experiment were brought onto the Western University campus in London, ON for testing, and then returned home with their owners. Each dog completed 20 choice trials.

2.2.1 Results

I conducted a one sample t-test on the performance scores of the ten dogs as compared to chance (50% accuracy) in order to determine if the dogs were finding the larger quantity above chance level.

A Shapiro-Wilk test of normality indicated that the data were normal, $W(9) = 0.92$, $p = .381$. The one sample t-test indicated that on average, dogs ($M = 70.50$, $SE = 4.07$) were able to find the larger quantity above chance, $t(9) = 4.44$, $p = .002$, $d = 1.40$ (a large effect size). See Figure 1.

2.2.2 Discussion

These data suggest that, contrary to the results of Horowitz et al. (2013), dogs were able to reliably smell a larger quantity of hot dog slices. My experiment used larger hot dog slices (2 cm wide by 2 cm long sections halved into semicylinders; halved again for smaller dogs, compared to 1.25 cm sections quartered into wedges in the Horowitz et al. (2013) experiment), and more trials per dog (20 trials each compared to 1 trial each in the Horowitz et al. experiment) than the Horowitz et al. experiment. I suggest that it was this increased amount of trials per dog that drove the difference in my findings from the Horowitz et al. experiment.

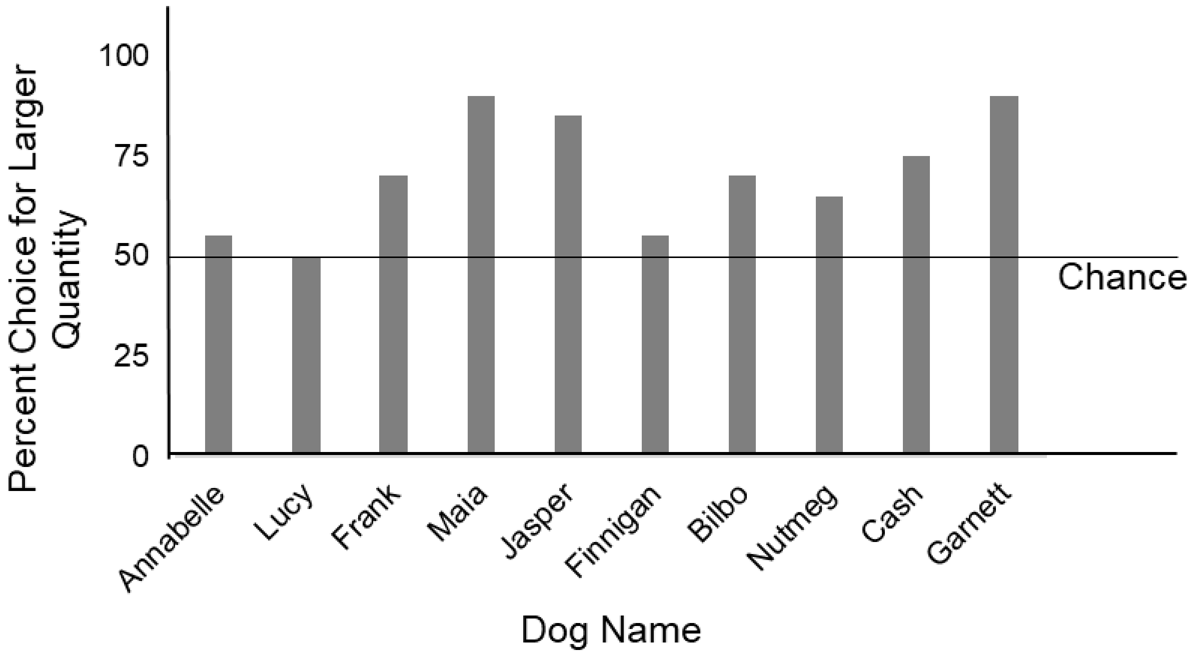

Figure 1. Percent choice for the larger quantity when given a choice between 1 and 5 hot dog slices. On average, dogs chose the larger quantity more often than they chose the smaller quantity.

2.3 Experiment 2

In the second experiment, dogs were offered a choice between several different hidden quantities of hot dog slices. The discriminations included 2 and 4 hot dog slices, 4 and 8 hot dog slices and 4 and 6 hot dog slices. I conducted this experiment to determine if dogs show either the distance effect or the ratio effect when discriminating olfactory quantities.

If the distance effect was shown, the dogs would have chosen the larger quantity with more accuracy on the discrimination of 4 and 8 hot dog slices than they would on the discriminations of 2 and 4 hot dog slices and 4 and 6 hot dog slices, because the distance between 4 and 8, which is 4, is larger than the distance between 2 and 4 and 4 and 6, which is 2. If the ratio effect was shown, the dogs would have chosen the larger quantity with more accuracy on the discriminations of 2 and 4 hot dog slices and 4 and 8 hot dog slices than they would on the discrimination of 4 and 6 hot dog slices, because the ratio difference of 2 and 4 and 4 and 8, which is 0.50, is smaller than the ratio difference of 4 and 6, which is 0.67.

Five of the dogs used in this experiment were brought onto campus for testing, and then returned home with their owners, and five of the dogs were tested in their homes by the experimenter. One dog, a bichon frise, was excluded from the analysis because he lost engagement and refused to complete the trials. All dogs included in the analysis completed eight choice trials of each of the 3 discriminations: 2 and 4 hot dog slices, 4 and 8 hot dog slices and 4 and 6 hot dog slices, totaling to 24 choice trials per dog.

2.3.1 Results

I conducted a one sample t-test in order to determine if the dogs were finding the larger quantity above chance level overall, regardless of the discrimination pair. Then I conducted a repeated measures ANOVA to determine if the performance of the dogs differed with discrimination pair.

A Shapiro-Wilk test of normality indicated that the data were normal, $W(9) = 0.87$, $p = .102$. The one sample t-test indicated that on average, dogs ($M = 63.75$, $SE =$

2.49) were able to find the larger quantity above chance, $t(9) = 5.53$, $p < .001$, $d = 1.75$ (a large effect size).

Mauchly's Test of Sphericity indicated that the assumption of sphericity had not been violated, $\chi^2(9) = 0.97$, $p = .889$, meaning variances between the conditions were assumed to be homogenous. The repeated measures ANOVA indicated no significant differences in the performance of the dogs among discrimination pairs, $F(2, 18) = 0.31$, $p = .737$, $\eta p^2 = 0.03$ (a small effect size). See Figure 2.

2.3.2 Discussion

Contrary to my hypothesis that dogs would conform to the predictions of the distance and ratio effects, I found no difference in performance across the tested discrimination pairs: 2 and 4 hot dog slices, 4 and 8 hot dog slices and 4 and 6 hot dog slices. This finding is also in contrast to the Plotnik et al. (2019) finding that elephants did conform to these effects when smelling quantities, as well as previous findings that dogs conform to these effects when presented with visual quantities (Ward & Smuts, 2007; Macpherson & Roberts, 2013; Petrazzini & Wynne, 2016). To test the possibility that my findings were due to quantity differences within discrimination pairs that were too small, I made these quantity differences more salient in Experiment 3.

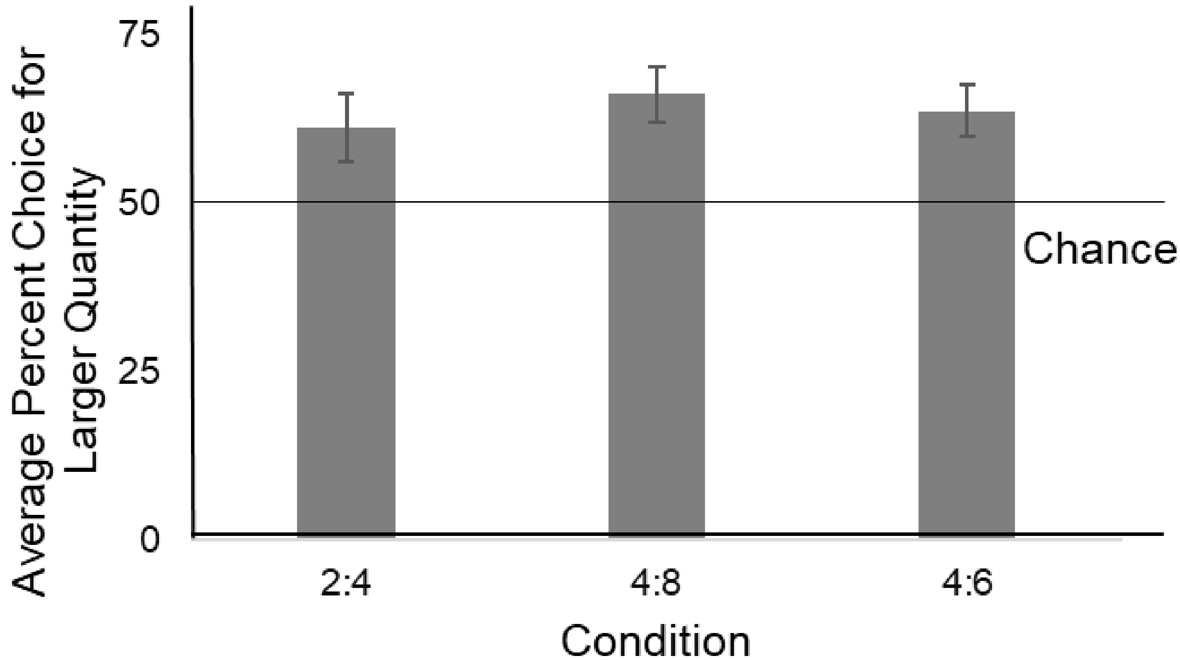

Figure 2. Average percent choice for the larger quantity at three different discrimination pairs. Dogs did not vary their performance with trial type but did choose the larger quantity overall. Error bars denote standard error.

2.4 Experiment 3

In the third experiment, dogs were offered a choice between several different hidden quantities of hot dog slices. The discriminations included 1 and 3 hot dog slices, 3 and 9 hot dog slices and 8 and 10 hot dog slices. I conducted this experiment to determine if dogs might show either the distance effect or the ratio effect when discriminating olfactory quantities with wider distance and ratio differences than used in Experiment 2.

If the distance effect is shown, the dogs should choose the larger quantity with more accuracy on the discrimination of 3 and 9 hot dog slices than they should on the discriminations of 1 and 3 hot dog slices and 8 and 10 hot dog slices, because the distance between 3 and 9, which is 6, is larger than the distance between 1 and 3 and 8 and 10, which is 2. Compared to Experiment 2, the difference between these distances, which is 4, is higher than the difference between the distances of 4 and 2, which is 2, used in Experiment 2. Experiment 3 then attempted to increase the saliency of the distance differences to the dogs.

If the ratio effect is shown, the dogs should choose the larger quantity with more accuracy on the discriminations of 1 and 3 hot dog slices and 3 and 9 hot dog slices than they should on the discrimination of 8 and 10 hot dog slices, because the ratio difference of 1 and 3 and 3 and 9, which is 0.33, is smaller than the ratio difference of 8 and 10, which is 0.8. Compared to Experiment 2, the difference between these ratio differences, which is 0.47, is higher than the difference between the ratio differences of 0.67 and 0.50, which is 0.17, used in Experiment 2. Experiment 3 then also attempted to increase the saliency of the ratio differences to the dogs.

All of the dogs used in this experiment were tested in their homes by the experimenter. All dogs completed four choice trials of each of the 3 discriminations: 1 and 3 hot dog slices, 3 and 9 hot dog slices and 8 and 10 hot dog slices, totaling to 12 choice trials per dog. By increasing the difference between the ratio differences and distance differences as compared to Experiment 2, the total number of hot dog slices a dog could get in 24 trials had increased. To avoid effects of satiation and/or overfeeding, the number of trials per dog was decreased from 24 trials in Experiment 2 to 12 trials in

Experiment 3. One dog, the Alaskan malamute/husky/German shepherd cross, was fed pieces of cooked ground beef (approximated to the size of the hot dog slices) instead of hot dog slices due to dietary restrictions.

2.4.1 Results

I conducted a one sample t-test in order to determine if the dogs were finding the larger quantity above chance level overall, regardless of the discrimination pair. Then I conducted a repeated measures ANOVA to determine if the performance of the dogs differed among discrimination pairs.

A Shapiro-Wilk test of normality indicated that the data were normal, W(9) = 0.85, $p = .064$. The one sample t-test indicated that on average, dogs (M = 57.50, SE = 4.88) were able to find the larger quantity above chance, $t(9) = 11.80$, $p < .001$, $d = 3.72$ (a large effect size).

Mauchly's Test of Sphericity indicated that the assumption of sphericity had not been violated, $\chi^2(9) = 0.87$, $p = .565$, meaning variances among the conditions were assumed to be homogenous. The repeated measures ANOVA indicated no significant difference in the performance of the dogs among discrimination pairs, $F(2, 18) = 1.33$, $p = .290$, $\eta p^2 = 0.13$ (a small effect size). See Figure 3. A composite of the results of Experiments 1-3 can be seen in Figure 4.

2.4.2 Discussion

Even at these widened distance and ratio differences, dogs showed no difference in performance across the tested discrimination pairs, consistent with Experiment 2. These results suggest that dogs do not conform to the distance and ratio effect when discriminating olfactory quantities as they do when discriminating visual quantities. If this is the case, it is likely that dogs do not use an approximate number system for olfactory quantities. The use of an object tracking system, which states quantities of 1-4 can be quickly identified as such (Piazza, 2010), may seem a more likely explanation given the lack of difference in performance across discrimination ratios (Petrazzini & Wynne, 2016; Feigenson et al., 2004), but my results do not show the expected breakdown in performance when discriminating quantities greater than 4 (Hauser et al., 2000; Feigenson et al., 2004). I reasonably conclude that, as observed by Petrazzini and Wynne (2016) when presenting dogs with visual quantities, dogs are relying on overall amount rather than number to make their choices when presented with olfactory quantities.

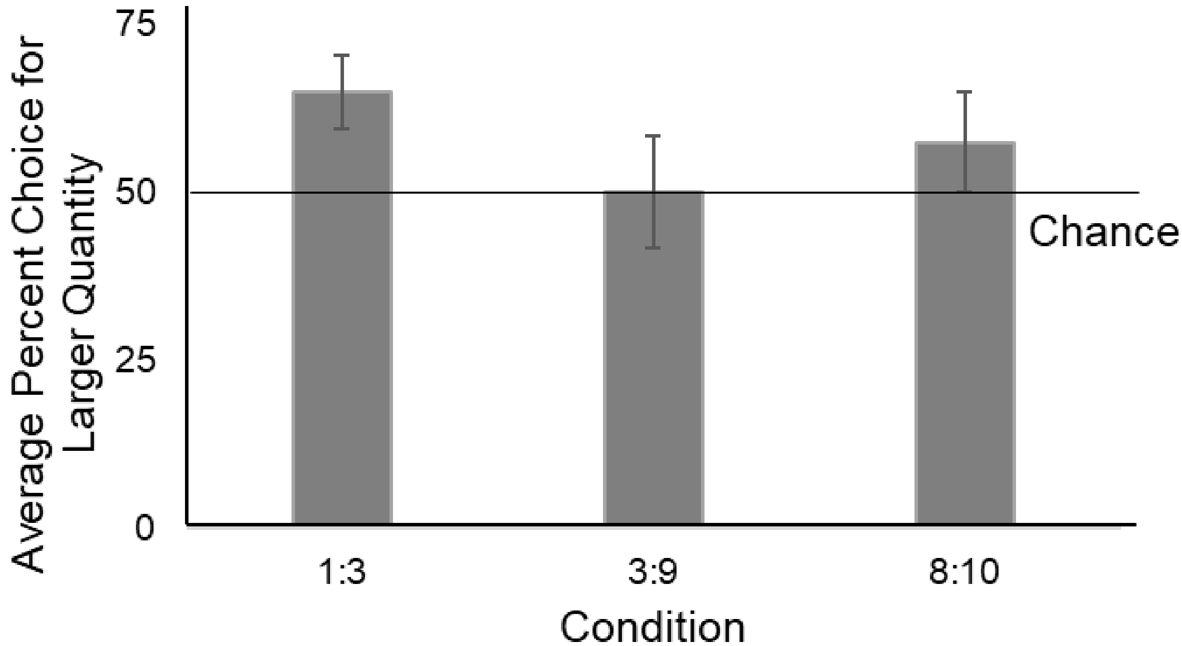

Figure 3. Average percent choice for the larger quantity at three different discrimination pairs. Dogs did not vary their performance with trial type but did choose the larger quantity above chance overall. Error bars denote standard error.

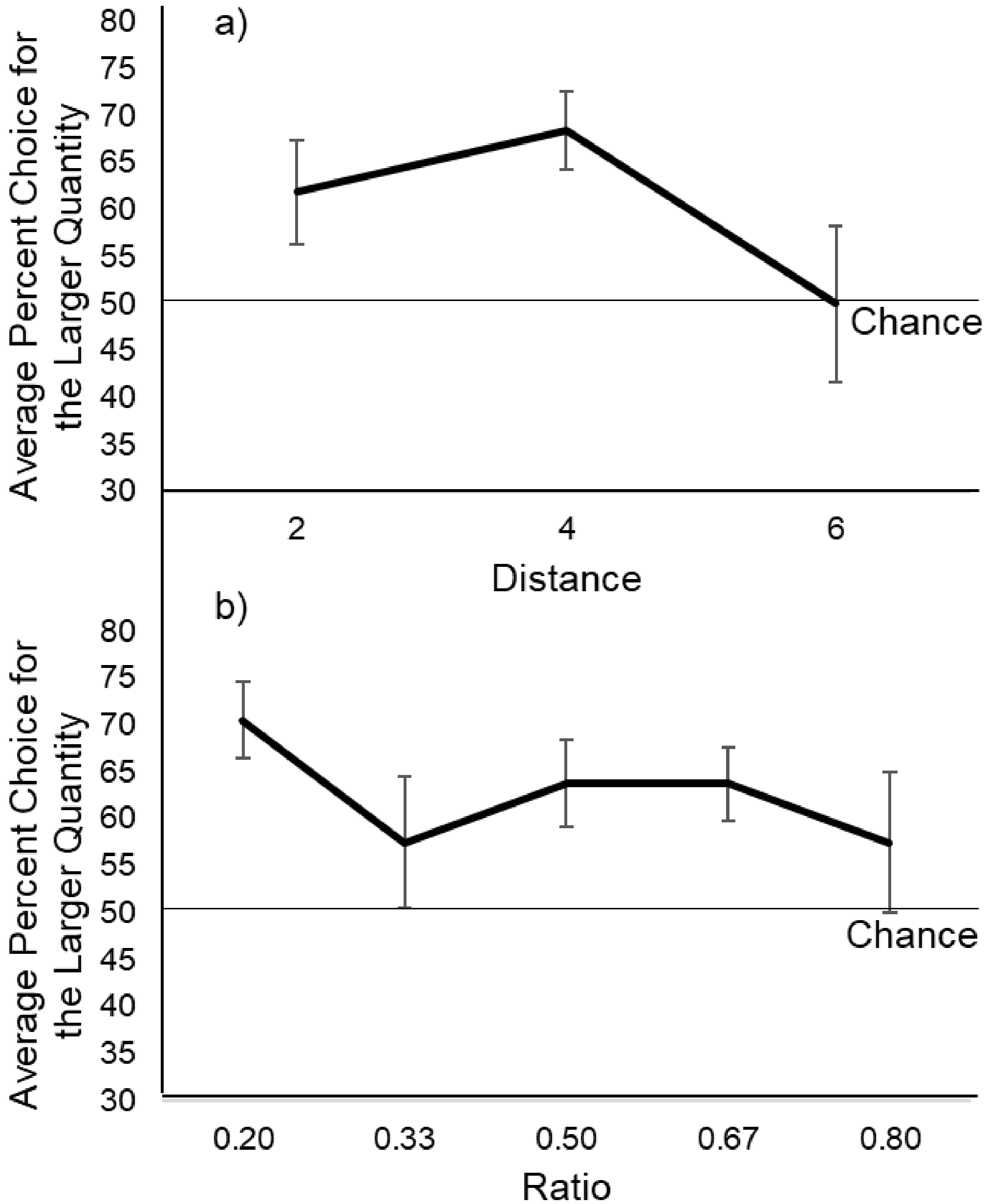

Figure 4. Average percent choice for the larger quantity as a function of a) increasing distance between the two values and b) increasing ratio of the values. Dogs did not reliably follow either the distance effect or the ratio effect when discriminating between olfactory quantities but did choose the larger quantity above chance overall. Data for this figure were taken from Experiment 1, Experiment 2, and Experiment 3. Error bars denote standard error.

2.5 Experiment 4

In the fourth experiment, dogs were offered a choice between a hidden quantity of 1 kibble piece and a hidden quantity of 5 kibble pieces in order to determine if they could smell the larger quantity. Each dog was tested using their own home-fed kibble brand, so kibble pieces varied in size and content but were the same for each dog. I conducted this experiment to see if dogs' performance for choosing the larger quantity would be decreased by discriminating quantities of a less preferred and less odorous item (kibble pieces as compared to hot dog slices).

Five of the dogs used in this experiment were new to this series of experiments and five of the dogs had been used in the previous experiments. All of the dogs were tested in their homes by the experimenter. Each of the 10 dogs completed an initial control trial followed by 12 test trials, totaling to 13 choice trials per dog.

The purpose of the control trial was to test if dogs preferred hot dog slices over their kibble pieces, which would indicate Experiment 4 trials were completed with a less-preferred food reward than Experiments 1-3 trials. In the control trial, the dog was shown a hot dog slice in one of the experimenter's open hands and a piece of its kibble in the other open hand. After being shown each open hand, the dog was allowed to choose between the hot dog slice and kibble piece, and its preference was recorded.

2.5.1 Results

I conducted a one sample t-test in order to determine if the dogs were finding the larger quantity above chance level. Then I conducted an independent samples t-test on the performance of the dogs in Experiment 4 compared to the performance of the dogs in Experiment 1 to determine if food type had an effect on performance.

In the initial control trial, 100% of the dogs chose the hot dog slice over the kibble piece. I took this as an indication of the dogs' preference for hot dog slices over their own kibble pieces.

A Shapiro-Wilk test of normality indicated that the test data were not normal, $W(9) = 0.81$, $p = .021$, indicating the results should be interpreted with caution. The one sample t-test indicated that on average, dogs ($M = 48.30$, $SE = 5.09$) were not able to find the larger quantity above chance, $t(9) = -0.33$, $p = .751$, $d = -0.10$ (a small effect size).

Comparing these results to those of Experiment 1, a Shapiro-Wilk test of normality indicated that the data were normal, $W(18) = 0.93$, $p = .171$. A Levene's test for equality of variances indicated that the variance of the dogs in Experiment 1 and the variance of the dogs in Experiment 4 were not significantly different, $F(1, 18) = 0.04$, $p = .836$. The independent samples t-test indicated that dogs in Experiment 1 ($M = 70.50$, $SE = 4.07$), that were receiving hot dog slices, located the larger quantity of food more often than dogs in Experiment 4 ($M = 48.30$, $SE = 5.09$), that were receiving kibble pieces, $t(18) = 3.22$, $p = .005$, $d = 1.44$ (a large effect size). See Figure 5.

2.5.2 Discussion

This finding supports the hypothesis that food type would affect dogs' performance for finding the larger quantity. This could be due to an influence of food type on either the dogs' motivation or capability to locate the larger quantity. Previous literature recognizes the impact of reinforcement type on motivation (Loveland & Olley, 1979; Markova & Ford, 2011), and my results showed a clear preference in dogs for hot dog slices over kibble pieces, but it is also possible that the two food types had differing levels of odour strength.

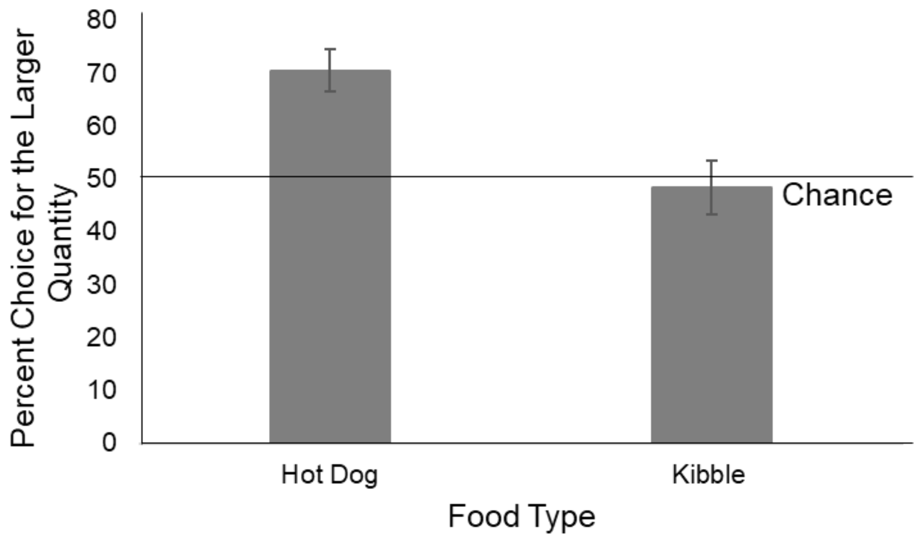

Figure 5. Average percent choice for the larger quantity as a function of food type. Dogs that were tested on the discrimination pair of one and five hot dog slices in Experiment 1 performed significantly better than dogs that were tested on the same discrimination pair with kibble pieces in Experiment 4. Error bars denote standard error.

2.6 Experiment 5

In the fifth experiment, dogs were offered a choice between several different hidden quantities of hot dog slices. The discriminations included 0 and 1 hot dog slice, 0 and 5 hot dog slices and 1 and 5 hot dog slices. I conducted this experiment to determine if dogs could associate the sound of hot dog slices being shaken in a container with the presence of hot dog slices in that container, and if they could discriminate larger amounts from smaller amounts by the amount of auditory stimulation present.

Instead of the dog smelling each container once each trial was set up and the blind was removed, the experimenter lifted each lidded container, one at a time, and shook them five times while the handler held the dog in its original position. This created a rattling sound when the lidded container had hot dog slices inside it, but not when it was empty. The experimenter always shook the lidded container to her left first, followed by the lidded container to her right. The five shakes were completed in approximately 5 s, with approximately one shake per second. After being shaken, each lidded container was placed back in its original position on one of the plates.

In addition to completing four test trials of each of the three discriminations: 0 and 1 hot dog slice, 0 and 5 hot dog slices and 1 and 5 hot dog slices, each of the dogs also completed 4 control trials, totaling to 16 choice trials per dog. The purpose of the control trials was to test if the dogs were finding the larger quantity through cues other than the auditory stimuli presented, such as experimenter bias or olfaction. The control trials used the 0 and 5 hot dog slices discrimination pair.

During control trials, the handler held the dog in place for 12 s as the experimenter remained motionless and continued to gaze between the containers. This amount of time was chosen to approximate the amount of time taken by the experimenter to shake both lidded containers on test trials. After both lidded containers had been shaken (test trials) or the dog had been held in place for 12 s (control trials), the handler held the dog in its original position (0.5 m back from the containers and centered between them) for an additional 3 s before releasing it to approach the containers.

I used grey, plastic containers, that measured 10 cm × 16 cm with a height of 5.5 cm, to hide the location of each quantity of hot dog slices. Each container had a lid that measured 10 cm × 16 cm. These containers did not have openings in the base. The lidded containers sat overturned (lid-side down) on top of white paper plates that had a diameter of 22.5 cm.

The same dogs from Experiment 4 were used for Experiment 5, so all of the dogs had been used in at least one of the previous experiments. All of these dogs were tested in their homes by the experimenter.

2.6.1 Results

I conducted a one sample t-test in order to determine if the dogs were finding the larger quantity above chance level overall, regardless of the discrimination pair. Then I conducted a repeated measures ANOVA to determine if the performance of the dogs differed among discrimination pairs or control trials.

A Shapiro-Wilk test of normality indicated that the data were normal, $W(9) = 0.90$, $p = .213$. The one sample t-test indicated that on average, dogs ($M = 73.30$, $SE = 4.61$) were able to find the larger quantity above chance in test trials, $t(9) = 5.06$, $p < .001$, $d = 1.60$ (a large effect size).

Mauchly's Test of Sphericity indicated that the assumption of sphericity had not been violated, $\chi^2(9) = 0.74$, $p = .796$, meaning variances between the groups were assumed to be homogenous. The repeated measures ANOVA indicated no significant differences in the performance of the dogs among trial types, $F(3, 27) = 0.38$, $p = .768$, $\eta p^2 = 0.04$ (a small effect size). See Figure 6.

2.6.2 Discussion

This test result indicates that although dogs were able to locate the larger quantity at an above chance level, the control trials used in this experiment were ineffective, meaning the dogs could have been finding the larger quantity through olfactory (or other) cues rather than auditory cues.

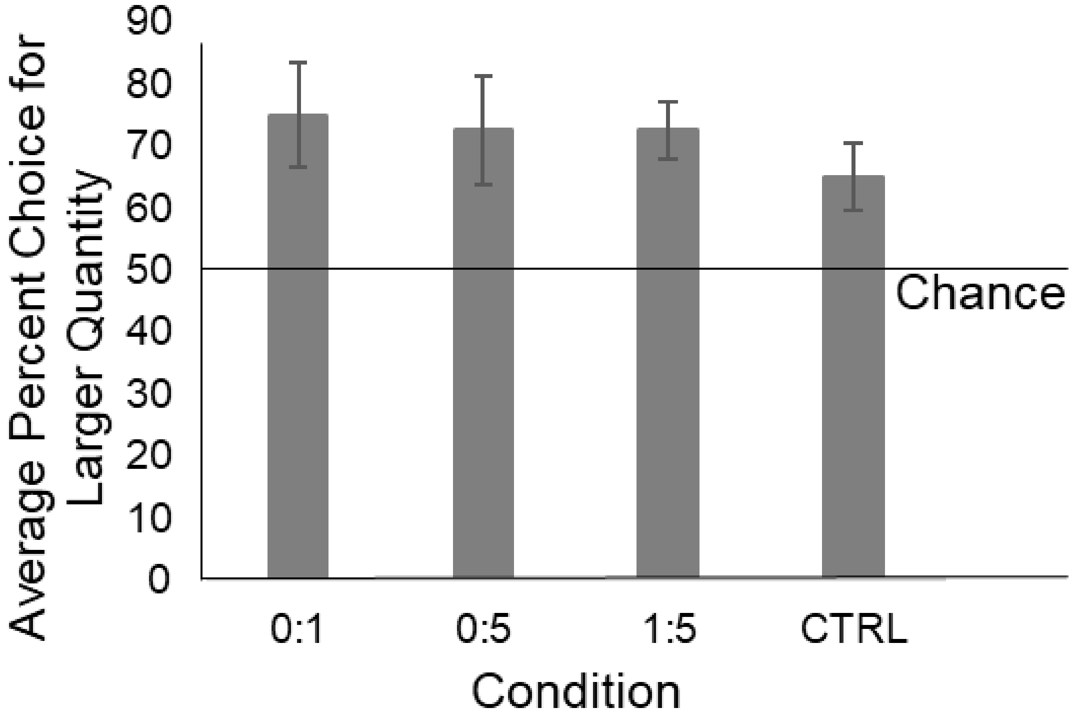

Figure 6. Average percent choice for the larger quantity at three different discrimination pairs as well as a control. Dogs did not vary their performance with trial type but did choose the larger quantity significantly above chance overall. Error bars denote standard error.

2.7 General Results

I ran a linear multilevel model on the data from the dogs in Experiment 1, Experiment 2 and Experiment 3. This level-one model allowed me to compare the performance of the dogs on the different discriminations across experiments. Individual dogs were entered as the model's subjects, and ratio discrimination was entered as a fixed effect predicting performance. In a second level-one model, experiment number rather than ratio discrimination was entered as a fixed effect predicting performance, in order to ensure testing conditions did not differ across experiments. Five level-two models replicated the conditions of model one but with additional fixed effects added in. Each of these models, in addition to ratio discrimination, added one of: age, individual dog, previous experience with cognition studies, hot dog size used in testing (large dogs were given larger semicylinder hot dog slices than small dogs) or spay/neuter status as a fixed effect predicting performance.

These models were run independently in order to prevent overfitting caused by too many parameters for the number of datapoints. In Babyak's (2004) introduction to overfitting, he advises that 3-4 datapoints per predictor is too few datapoints to avoid overfitting of a model. My first model was run with approximately 8 datapoints per parameter (70 datapoints per predictor variable). My second model was run with 14 datapoints per parameter (70 datapoints per predictor variable). Subsequent models were run with approximately 7, 2, 6, 7 and 6 datapoints per parameter, respectively (35 datapoints per predictor variable). Neumann (2016) mentions this method of running several simple models rather than one or a few more complex models to prevent overfitting, but cautions that because this would allow us to single out the best fitting model of the group, assumptions from this model about the larger population outside the study's sample size could lead to overestimates of performance. However, given my results below, this issue is of little concern.

Tests for the possible effects of age, individual dog, previous experience, hot dog size and spay/neuter status were not performed on the data from the dogs in Experiment

4, Experiment 5, or Experiment 6. These data could not be amalgamated into a multilevel model because of differences in procedure, and correlations/t-tests performed for each of these experiments would have very small sample sizes. I decided the results from the multilevel models for the amalgamated data from Experiment 1, Experiment 2 and Experiment 3 would be a better indicator of the possible effects of these variables.

The first multilevel model indicated that ratio discrimination was not a significant predictor of performance, $F(6, 63) = 1.32$, $p = .262$. See Figure 4. All subsequent models triggered a warning that the final Hessian matrix was not positive definite, meaning the results should be interpreted with caution. This warning is often due to redundancies between variables. In this case, it is likely due to the factors of experiment number, age, individual dog, previous experience, hot dog size and spay/neuter status all being variables that were redundant with the subject variable of individual dog.

The second model indicated that experiment number was also not a significant predictor of performance, $F(2, 67) = 2.11$, $p = .129$. When ratio discrimination and age were entered as fixed effects, neither ratio, $F(6, 57) = 1.31$, $p = .266$, nor age, $F(1, 57) = 0.01$, $p = .927$, was a significant predictor of performance. When ratio discrimination and individual dog were entered as fixed effects, neither ratio, $F(4, 36) = 1.00$, $p = .420$, nor individual dog, $F(27, 36) = 1.19$, $p = .310$, was a significant predictor of performance. When ratio discrimination and previous experience were entered as fixed effects, neither ratio, $F(6, 61) = 1.71$, $p = .135$, nor previous experience, $F(2, 61) = 1.32$, $p = .275$, was a significant predictor of performance. When ratio discrimination and hot dog size were entered as fixed effects, neither ratio, $F(6, 62) = 1.19$, $p = .324$, nor hot dog size, $F(1, 62) = 0.001$, $p = .972$, was a significant predictor of performance. When ratio discrimination and spay/neuter status were entered as fixed effects, neither ratio, $F(6, 61) = 1.26$, $p = .290$, nor spay/neuter status, $F(2, 61) = 0.02$, $p = .985$, was a significant predictor of performance. See Figure 7.

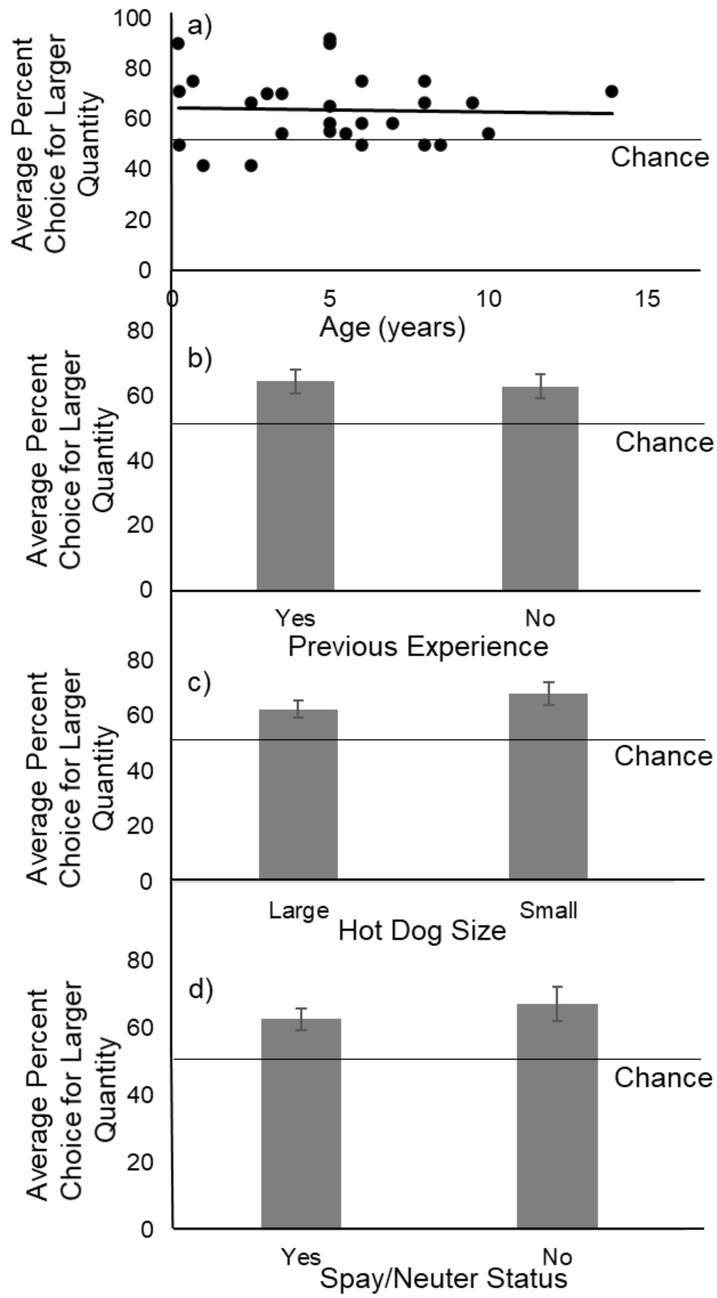

Figure 7. Average percent choice for the larger quantity as a function of a) age, b) previous experience, c) hot dog size, and d) spay/neuter status. Performance did not vary with any of these factors. Data for this figure were taken from Experiment 1, Experiment 2 and Experiment 3. Error bars denote standard error.

Chapter 3

3 Discussion and Conclusions

3.1 General Discussion

In my first experiment, I found that contrary to the results of Horowitz et al. (2013), dogs were able to reliably smell a larger quantity of hot dog slices, likely as a result of the increased number of trials in this experiment. Dogs may not have immediately understood that one container had more food than the other. Many of the tested dogs would pace between containers, look back to their owners for guidance, or directly approach the experimenter rather than either container upon being released to make a choice in the early trials, but had the opportunity over several trials to learn that the larger quantity of hot dog slices could be identified by olfactory cues. Most dogs learned this rule very quickly over just a few trials, but dogs in the Horowitz et al. experiment did not have this opportunity.

It is worth noting that Horowitz et al. (2013) intentionally tested each dog on only one trial. Their research question clearly specifies they aimed to determine how much dogs without olfactory training rely on olfactory cues. A single trial task is a logical choice for this question because it measures a dog's default response to a novel problem. However, I would argue that although 20 trials gives a dog an opportunity to learn how the task works, it does not offer much opportunity to improve olfactory skills.

Therefore, I expect that although dogs, on average, are reliably capable of locating a larger quantity based on olfactory cues, as per my results, it is not their default mode of problem-solving when presented with a novel task by a human, as the Horowitz et al. (2013) results suggest. For most pet dogs, novel problems presented by humans would be solvable primarily through visual (ex. luring) or auditory (ex. verbal commands) modules. However, although dogs may not associate human-presented problems with olfactory cues, they may associate other problems they encounter in their daily lives with olfactory cues, for example gaining information about other dogs (Bekoff, 2018). This means that dogs would maintain the ability to use olfactory cues so long as environmental information suggested this was the most appropriate module for them to apply to a given problem.

This theory is further supported by the observation in the Horowitz et al. (2013) paper that prior to making a selection, dogs paid more attention to the paper plate containing the larger quantity of hot dog slices. This observation suggests that dogs might have been able to smell the difference in quantity but did not understand what was being requested of them and so relied on their previous experience with human-presented problems, which was that these problems could be solved through visual or auditory modalities. This theory also aligns with the Horowitz et al. replication of Prato-Previde et al.'s (2008) results, wherein dogs relied on human cues to make a choice, as well as with Plotnik et al.'s (2019) results, wherein elephants were able to smell the larger quantity with an 80% success rate in 12 trials (although their single trial success rate is unclear).

The results of my second and third experiments are less well-aligned with those of Plotnik et al. (2019), in which elephants were found to show both the distance and ratio effects when comparing olfactory quantities. Contrary to my hypothesis that dogs would also conform to the predictions of the distance and ratio effects, I found no difference in performance across the tested discrimination pairs. Previous findings suggest that dogs do conform to these effects when presented with visual quantities (Ward & Smuts, 2007; Macpherson & Roberts, 2013; Petrazzini & Wynne, 2016). Thus, it is likely that dogs do not use an approximate number system or object tracking system for olfactory quantities, but rather rely on an all-or-none response system.

If dogs were finding the larger quantity in these experiments by discriminating mass of food rather than number of items, then they may have relied on the number of olfactory receptors activated as a result of sniffing each container. If this were the case, they may not have followed the distance and ratio effects because the number of molecules emitted from each container may not have been linear to one another. That is, if hot dog slices in the container with the greater quantity were piled atop one another (therefore producing less exposed hot dog slice surface area), then they may have emitted a lesser number of molecules for the dog to sniff than would be predicted based on a linear relationship between the quantities, or approximate number system. Further, some scents can be perceived differently at different concentrations, because different combinations of olfactory receptors are activated at different concentrations of the same scent (Malnic et al., 1999), meaning that a greater quantity of hot dog slices may actually smell differently, not just stronger, than a smaller quantity of hot dog slices. This would support the idea of an all-or-none response system that treats quantities as continuous rather than a system that conformed to the distance and ratio effects, treating quantities discretely. Another possibility is that dogs do conform to the distance and/or ratio effects when discriminating olfactory quantities, but at a very low stimulus sensitivity. For example, dogs might discriminate100 hot dog slices from 50 hot dog slices much more easily than they would discriminate 4 hot dog slices from 2 hot dog slices but testing a sensitivity of this level was not feasible within the scope of this study.

In my fourth experiment, I investigated if the food type used as reinforcement could have an impact on performance. As expected, I found that the dogs in Experiment 1, reinforced with hot dog slices, chose the larger quantity significantly more often than the dogs in Experiment 4, reinforced with kibble pieces, suggesting food type does influence performance. If this difference in performance is because different foods elicit more pronounced discrimination of olfactory quantities, then it is possible that the distance and/or ratio effect may not only be shown at wider distance and ratio differences, but also shown more effectively with different food types used as reinforcement. In this case, these numerical discrimination effects may be shown at narrower distance and ratio differences when a more valued food type is used as reinforcement.

Differences in odour strength could mean that the dogs were able to smell hot dog slices more easily than kibble pieces simplifying their discrimination. Different combinations and numbers of olfactory receptors are activated by different scents, meaning that some scents can be detected at lower concentrations than other scents (Malnic et al., 1999).

The reverse could also be argued; that because the hot dog slices smelled more strongly than the kibble pieces, dogs were overwhelmed by the large amount of scent emitted by the hot dog slices and therefore found kibble piece quantities easier to discriminate. This would be consistent with the magnitude effect, that larger overall quantities (in this case, the overall strength of odour) are harder to discriminate from one another than smaller overall quantities when distance is held constant. Although animals commonly conform to this numerosity effect with visual quantities (Dehaene et al., 1998), this explanation does not fit my results.

Regardless, the observed effect of food type used as reinforcement on performance in my results could be due to an effect of food type used as reinforcement on motivation, an effect of food type used as reinforcement on the physical ability to discriminate the quantities, or some combination of the two. Future work could separate and quantify these factors.

In my fifth experiment, I extended this work to the auditory modality. Contrary to my prediction, I found no evidence that dogs were able to discriminate larger quantities from smaller quantities of hot dog slices when receiving auditory information. The tested discrimination pairs, 0 and 1 hot dog slices, 0 and 5 hot dog slices and 1 and 5 hot dog slices, did not allow me to test for the presence of the distance or ratio effects. Rather, given the limited amount of research into whether animals, and specifically dogs, are able to respond to sound as a cue to food and further discriminate quantity through sound, I sought to address these questions instead. Beran (2012) did address the ability of chimpanzees to hear quantity but presented food items in a container sequentially rather than altogether. In order for the chimps in the study to find the larger quantity, they had to count the number of food items dropped rather than hear that one container, when shaken, had more food items in it than the other container. Plotnik et al. (2014) addressed the ability of elephants to understand sound as a cue to food but not their ability to hear quantity. In order for the elephants in the study to find the larger quantity, they had to choose the container that produced sound; the other container was empty and produced no sound when shaken. The elephants did not exceed chance level on this task. In dogs, the ability to respond to sound as a cue to food has not been separated from the ability to respond to human direction as a cue to food (Hare et al., 2002; Bräuer et al., 2006). To my knowledge, no work in dogs has explored the ability to discriminate quantities greater than 0 through strictly auditory cues.

Based on the above-chance performance of the dogs on the control trials in Experiment 5, I cannot conclude that the dogs were not finding the larger quantity in the other trials through means of olfactory cues or experimenter bias. In my earlier experiments designed to test the ability of dogs to use olfactory cues to locate quantities of food, the dogs were given the opportunity to smell each container at close proximity and still only found the larger quantity 60-70% of the time on average. In Experiment 5, dogs did not receive the opportunity to smell either container at close proximity. They stood approximately 0.5 m away while auditory information was presented and then chose a container. It seems unlikely that an approximate 70% success rate for finding the larger quantity would have been maintained through olfactory cues with this impaired opportunity to smell the containers. Given that dogs only received 4 control trials in Experiment 5, a single choice above chance level drove a dog’s score on control trials from 50% accuracy for the larger quantity to 75% accuracy for the larger quantity. An exploratory pilot study of a single dog given 10 control trials and 10 test trials of the 0 and 5 hot dog slices discrimination yielded encouraging results regarding the efficiency of the control trials in Experiment 5. Based on these observations, further investigation into how dogs were finding the larger quantity in this paradigm could be beneficial.

3.2 Conclusions

3.2.1 Cognitive Implications

Overall, this study is the first to provide an in-depth analysis of dogs’ ability to understand quantity across non-visual modalities. I found evidence that dogs were quite good at discriminating larger quantities from smaller quantities when cues to these quantities were presented in the olfactory modality, but not the auditory modality. In contrast to dogs’ adherence to the distance and ratio effects when presented with visual quantities (Ward & Smuts, 2007; Petrazzini & Wynne, 2016; Macpherson & Roberts, 2013), I found no evidence that dogs performed more accurately when quantities were farther apart or had a lower ratio (when the smaller quantity is divided by the larger quantity) when presented with olfactory cues. I found no evidence in this study that dogs' age, previous experience, or spay/neuter status affected their ability to understand quantity. The lack of an effect of age is consistent with recent findings that suggest simple numerical discrimination develops early in puppies (Petrazzini et al., 2020).

Based on the consistent finding that distance and ratio effects are found in the visual modality (Ward & Smuts, 2007; Petrazzini & Wynne, 2016; Macpherson & Roberts, 2013), my findings suggest that in dogs, the ability to perceive quantity may differ between modalities. This contrasts with the abstract sense of number in humans, in which quantities can be perceived comparably well across different modalities and formats (ex. cues presented altogether versus sequentially) (Arrighi et al., 2014). Beran's (2012) work shows chimps are also capable of perceiving auditory quantities in different formats and that this performance is comparable to their visual perception of number. Alternatively, dogs may have adapted a sense of quantity separately for separate modalities based on differing needs from other species.

For instance, it may have been useful for ancestral dogs to distinguish visual quantities in detail, eventually leading to the development of an approximate number system, when deciding whether to pursue a potential source of food when weighed against other potential sources or risk factors. However, this ability may have been less useful in other modalities, leading dogs to rely more heavily on an all-or-none response system. Olfactory and auditory cues could be used from a distance to find, track, and investigate potential resources while vision could be used in closer range to make the final decision to commit or not commit to an interaction with the source of the cue. This interaction could consist of actively hunting prey or engaging in intra- or interspecies competition and accepting the risks of taking part in these activities. Simpler levels of perception would be sufficient for initially detecting a resource, as well as pursuing smaller, low-risk hunting expeditions such as determining the approximate quantity of baby rabbits in an underground burrow, but a higher cognitive functioning may have been necessary when weighing the potential risks of an interaction with larger, above ground prey.

By maintaining only a rudimentary level of perception in the olfactory and auditory modalities, cognitive space could be saved for other functions. However, if these senses were to be used at a greater distance from the source of the cue, they would need to be stronger than vision in order to perceive such cues from a greater distance, indicating a trade-off between the strength of a sense and the strength of the cognitive function accompanying that sense. Consistent with this theory, although dogs have less-detailed vision than humans, their hearing is superior (Horowitz, 2009), and a preference is shown for using olfactory cues over visual cues when tracking (Gazit & Terkel, 2003). In both dogs and wolves, sensitivity to olfactory and auditory cues develops before sensitivity to vision develops (Lord, 2012). The earlier and stronger development of these senses is not only relevant to locating such resources as food, but also to long-distance social communication (Theberge & Falls, 1967; Harrington & Asa, 2007).

As mentioned by Plotnik et al. (2014), research into the cognitive abilities of animals for perceiving quantity in different modalities creates an important groundwork for the design of future studies in animal cognition, especially in animals that may not rely on visual cues in their natural environments. For instance, in addition to my finding that dogs may perceive quantities differently across modalities, my finding that food type affects performance is important to designing future studies, because more motivating food types may be necessary to elicit more complex behaviours. These same animals may not be willing to work as hard for a lesser reward, even if the quantity of that reward is consistent. Furthermore, this finding has implications for cross-study comparisons of performance both between and within species that use different food types as rewards. If food type influences performance, then it is important that comparative work use food types of equal value to the subjects, but quantifying the value of a hot dog to a dog compared to the value of a grape to a chimp could be a difficult endeavor. Within species, the problem can be addressed much easier through preference studies. The influence of individual preference on performance is another area that could benefit from additional study.

3.2.2 Practical Implications

In a practical sense, this work is relevant to both working and pet dogs. If my finding of food type influencing performance is due to certain food types being easier to discriminate than others rather than due to a motivational issue, then scent dogs may have greater success following certain scents over others. In support of this view that the influence of food type is due to the ability to detect the scent, previous research has shown that trained scent dogs perform better on scents that are newer, and therefore stronger, than older scents (King et al.,1964; Cablk et al., 2008). Future research could break down this question of whether food type influences performance due to motivation differences or strength of cue differences by further exploring the auditory modality. Following the general procedure used in Experiment 5, in which containers had lids but no openings to prevent odour escape, dogs could be offered a choice between an equal quantity of hot dog slices or kibble pieces. My results indicate that dogs prefer hot dog slices over kibble pieces, but in this design the hard pieces of kibble would create more auditory stimuli than the hot dog slices hitting the container. Therefore, strength of odour would be removed from the design and the food type that yielded stronger stimuli (louder noise) would not be the preferred food type, thus separating the confound of strength of cue and motivation. However, additional care would be required to prevent the escape of odour cues, as my Experiment 5 results indicated that olfactory cues may have influenced the dogs' performance in this experiment,

The finding that most dogs are quite good at distinguishing larger quantities from smaller quantities when following olfactory cues is also relevant to trained scent dogs. These dogs are traditionally trained to signal in response to detecting a scent, regardless of the quantity associated with that scent. Although this method is critical for detecting moving targets, such as missing children, it may be less necessary to drug detection dogs, wherein handlers may want to focus their efforts on larger amounts of narcotics only. Lit and Crawford (2006) have shown that scent dogs trained to a single scent perform better than scent dogs trained to detect multiple scents, so it may also be possible that scent dogs perform better when trained to detect only large quantities of a single scent.

For the average pet owner, understanding that dogs do not seem to conform to the distance or ratio effects when responding to olfactory or auditory cues but do seem to understand the more fundamental “larger than” or “smaller than” rule can be helpful to obedience training. Often in dog training, large accomplishments are rewarded with a “jackpot”, or an especially large amount of treats (Wye, 2010). One way that dogs could know they are, or will be, receiving more treats than usual is through the olfactory cues of smelling a quantity of treats in their handler’s hand, or the auditory cues of hearing a quantity of treats being removed from the bag and held in their handler’s hand. My research suggests that dogs would understand an especially large amount of treats as simply more treats than usual and not perform better for certain amounts of jackpot over others because neither the distance nor the ratio effect was shown. That is, a dog should be just as good at discriminating 4 treats from the usual 2 as they are at discriminating 8 treats from the usual 4. These non-visual cues could be important to motivating dogs with jackpots, both because some dogs may be too excited when receiving treats to perceive any form of visual information about them and because cues are responded to quicker and with more accuracy when presented in several sensory modalities. In fact, many species may even be adapted to respond better to these multimodal, rather than unimodal, cues (Rowe, 1999).

3.2.3 Concluding Statement

In conclusion, this study presents new information regarding the sensory modalities of dogs. To my knowledge, it is the first set of experiments to test numerical discrimination effects in the olfactory modality and the first to use a two-way object choice paradigm to test dogs’ ability to perceive auditory cues presented altogether rather than sequentially. My findings in these areas raise the possibility that dogs have evolved separate systems for perceiving quantity in separate modalities. Further, my results stress the importance of choosing an appropriate source of reinforcement in cognition studies.

References

Arrighi, R., Togoli, I., & Burr, D. C. (2014). A generalized sense of number. *Proceedings of the Royal Society B: Biological Sciences, 281(1797),* 1-7. doi: 10.1098/rspb.2014.1791

Babyak, M. A. (2004). What you see may not be what you get: A brief, nontechnical introduction to overfitting in regression-type models. *Psychosomatic Medicine, 66(3),* 411-421. doi: 10.1097/01.psy.0000127692.23278.a9

Bach, J. P., Lüpke, M., Dziallas, P., Wefstaedt, P., Uppenkamp, S., Seifert, H., & Nolte, I. (2013). Functional magnetic resonance imaging of the ascending stages of the auditory system in dogs. *BMC Veterinary Research, 9(1),* 210. doi: 10.1186/1746-6148-9-210

Bekoff, M. (2018). *Canine confidential: Why dogs do what they do.* Chicago, IL: University of Chicago Press.

Benson-Amram, S., Gilfillan, G., & McComb, K. Numerical assessment in the wild: Insights from social carnivores. (2017). *Philosophical Transactions of the Royal Society B, 373,* 20160508. doi: 10.1098/rstb.2016.0508

Beran, M. J. (2001). Summation and numerousness judgments of sequentially presented sets of items by chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology, 115(2),* 181-91. doi: 10.1037/0735-7036.115.2.181

Beran, M. J. (2012). Quantity judgements of auditory and visual stimuli by chimpanzees (*Pan troglodytes*). *Journal of Experimental Psychology: Animal Behavior Processes, 38(1),* 23-29. doi:10.1037/a0024965

Boysen, S. T. & Berntson, G. G. (1989). Numerical competence in a chimpanzee (*Pan troglodytes*). *Journal of Comparative Psychology, 103(1),* 23-31. doi: 10.1037/0735-7036.103.1.23

Brannon, E. M. & Merritt, D. J. (2011). Evolutionary foundations of the approximate number system. In S. Dehaene & E. Brannon (Eds.), *Space, time and number in* *the brain: Searching for the foundations of mathematical thought* (pp. 207–224). Elsevier Academic Press. doi: 10.1016/B978-0-12-385948-8.00014-1

Bräuer, J., Kaminski, J., Riedel, J., Call, J., & Tomasello, M. (2006). Making inferences about the location of hidden food: Social dog, causal ape. *Journal of Comparative Psychology, 120(1),* 38-47. doi: 0.1037/0735-7036.120.1.38

Cablk, M. E., Sagebiel, J. C., Heaton, J. S., & Valentin, C. (2008). Olfaction-based detection distance: A quantitative analysis of how far away dogs recognize tortoise odor and follow it to source. *Sensors, 8(4),* 2208-2222. doi: 10.3390/s8042208

Capaldi, E. J., Miller, D. J., & Alptekin, S. (1989). A conditional numerical discrimination based on qualitatively different reinforcers. *Learning and Motivation, 20(1),* 48-59. doi: 10.1016/0023-9690(89)90031-3

Dacke, M. & Srinivasan, M. V. (2008). Evidence for counting in insects. *Animal Cognition, 11(4),* 683-689. doi: 10.1007/s10071-008-0159-y

Dehaene, S., Dehaene-Lambertz, G., Cohen, L. (1998). Abstract representations of numbers in the animal and human brain. *Trends in Neurosciences, 21(8),* 355-361. doi: 10.1016/S0166-2236(98)01263-6

Duranton, C. & Horowitz, A. (2019). Let me sniff! Nosework induces positive judgment bias in pet dogs. *Applied Animal Behaviour Science, 211,* 61-66. doi: 10.1016/j.applanim.2018.12.009

Fahnestock, M., Marchese, M., Head, E., Pop, V., Michalski, B., Milgram, W. N., & Cotman, C. W. (2012). BDNF increases with behavioral enrichment and an antioxidant diet in the aged dog. *Neurobiology of Aging, 33(3),* 546-554. doi: 10.1016/j.neurobiolaging.2010.03.0194

Feigenson, L., Dehaene, S., & Spelke, E. (2004). Core systems of number. *Trends in Cognitive Sciences, 8(7),* 307-314. doi: 10.1016/j.tics.2004.05.002

Gadbois, S. & Reeve, C. (2014). Canine olfaction: Scent, sign, and situation. In: Horowitz, A. (eds) Domestic dog cognition and behavior. Springer, Berlin, Heidelberg. doi: 10.1007/978-3-642-53994-7_1

Gazit, I. & Terkel, J. (2003). Domination of olfaction over vision in explosives detection by dogs. *Applied Animal Behaviour Science, 82(1),* 65-73. doi: 10.1016/S0168-1591(03)00051-0

Gazzola, A., Vallortigara, G., & Pellitteri-Rosa, D. (2018). Continuous and discrete quantity discrimination in tortoises. *Biology Letters, 14(12),* 1-4. doi: doi.org/10.1098/rsbl.2018.0649

Graham, L., Wells, D. L., & Hepper, P. G. (2005). The influence of olfactory stimulation on the behaviour of dogs housed in a rescue shelter. *Applied Animal Behaviour Science, 91(1-2),* 143-153. doi: 10.1016/j.applanim.2004.08.024

Hackner, K. & Pleil, J. (2017). Canine olfaction as an alternative to analytical instruments for disease diagnosis: Understanding 'dog personality' to achieve reproducible results. *Journal of Breath Research, 11(1),* 012001. doi: 10.1088/1752-7163/aa5524.

Harrington, F. H. & Asa, C. S. (2003). Wolf communication. In Mech, L. D. & Boitani, L. (Ed.), *Wolves: Behavior, ecology, and conservation* (pp. 66–103). Chicago, IL: University of Chicago Press.

Hauser, M. D., Carey, S., & Hauser, L. B. (2000). Spontaneous number representation in semi-free-ranging rhesus monkeys. *Proceedings of the Royal Society B: Biological Sciences, 267(1445),* 829-33. doi: 10.1098/rspb.2000.1078

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

Haxby, J. V., Gobbini, M. I., Furey, M. L., Ishai, A., Schouten, J. L., & Pietrini, P. (2001). Distributed and overlapping representations of faces and objects in ventral temporal cortex. *Science, 293(5539),* 2425-2430. doi:

10.1126/science.1063736Horowitz, A. (2009). *Inside of a dog: What dogs see, smell, and know.* New York City, NY: Scribner.

Horowitz, A., Hecht, J., and Dedrick, A. (2013). Smelling more or less: Investigating the olfactory experience of the domestic dog. *Learning and Motivation, 44(4),* 207-217. doi: 10.1016/j.lmot.2013.02.002

Kalmus, H. (1955). The discrimination by the nose of the dog of individual human odours and in particular of the odours of twins. *The British Journal of Animal Behaviour, 3(1),* 25-31. doi: 10.1016/S0950-5601(55)80072-X

King, J. E., Becker, R. F., & Markee, J. E. (1964). Studies on olfactory discrimination in dogs: (3) Ability to detect human odour trace. *Animal Behaviour, 12(2-3),* 311-315. doi: 10.1016/0003-3472(64)90017-X

Krichbaum, S., Rogers, B., Cox, E., Waggoner, L. P., & Katz, J. S. (2020). Odor span task in dogs (*Canis familiaris*). *Animal Cognition, 23(3),* 571–580. doi: 10.1007/s10071-020-01362-7

LeDoux, J. E., Sakaguchi, A., & Reis, D. J. (1984). Subcortical efferent projections of the medial geniculate nucleus mediate emotional responses conditioned to acoustic stimuli. *Journal of Neuroscience, 4(3),* 683-698. doi: 10.1523/JNEUROSCI.04-03-00683.1984

Lit, L. & Crawford, C. A. (2006). Effects of training paradigms on search dog performance. *Applied Animal Behaviour Science, 98(3-4),* 277-292. doi: 10.1016/j.applanim.2005.08.022

Lo, K. H., Macpherson, K., MacDonald, H., & Roberts, W. A. (2020.). A comparative study of memory for olfactory discriminations: Dogs (*Canis familiaris*), rats (*Rattus norvegicus*), and humans (*Homo sapiens*). *Journal of Comparative Psychology, 134(2), 170-179.* doi: 10.1037/com0000205

Lo, K. H. & Roberts, W. A. (2019). Dogs (*Canis familiaris*) use odor cues to show episodic-like memory for what, where, and when. *Journal of Comparative Psychology, 133(4),* 428-441. doi: 10.1037/com0000174

Lord, K. (2012). A comparison of the sensory development of wolves (*Canis lupus lupus*) and dogs (*Canis lupus familiaris*). *Ethology, 119(2),* 110-120. doi: 10.1111/eth.12044

Loveland, K. K. & Olley, J. G. (1979). The effect of external reward on interest and quality of task performance in children of high and low intrinsic motivation. *Child Development, 50(4),* 1207-1210. doi: 10.2307/1129350

Macpherson, K. & Roberts, W. A. (2013). Can dogs count? *Learning and Motivation, 44(4),* 241-251. doi: 10.1016/j.lmot.2013.04.002

Malnic, B., Hirono, J., Sato, T., & Buck, L. B. (1999). Combinatorial receptor codes for odors. *Cell, 96(5),* 713-723. doi: 10.1016/S0092-8674(00)80581-4

Markova, G. & Ford, C. (2011). Is money the panacea? Rewards for knowledge workers. *International Journal of Productivity and Performance Management, 60(8),* 813-823. doi: 10.1108/17410401111182206

McHugh, M. L. (2013). The Chi-square test of independence. *Biochemia Medica,* 23(2), 143-149. doi: 10.11613/BM.2013.018

Milgram, N. W. (2003). Cognitive experience and its effect on age-dependent cognitive decline in beagle dogs. *Neurochemical Research, 28(11),* 1677-1682. doi: 10.1023/A:1026009005108

Neumann, J. (2016). Points of significance: Model selection and overfitting. *Nature Methods, 13(9),* 703-704. doi: 10.1038/nmeth.3968

Overall, K. L. & Dyer, D. (2005). Enrichment strategies for laboratory animals from the viewpoint of clinical veterinary behavioral medicine: emphasis on cats and dogs. *Institute for Laboratory Animal Research, 46(2),* 202-216. doi: 10.1093/ilar.46.2.202

Pattison, K. F. & Zentall, T.R. (2014). Suboptimal choice by dogs: When less is better than more. *Animal Cognition, 17,* 1019. doi: 10.1007/s10071-014-0735-2

Petrazzini, M. E. M., Mantese, F., & Prato-Previde, E. (2020). Food quantity discrimination in puppies (*Canis lupus familiaris*). *Animal Cognition, 23,* 703-710.

Petrazzini, M. E. M. & Wynne, C. D. L. (2016). What counts for dogs (Canis lupus familiaris) in a quantity discrimination task? *Behavioural Processes, 122,* 90-97. doi: 10.1016/j.beproc.2015.11.013

Piazza, M. (2010). Neurocognitive start-up tools for symbolic number representations. *Trends in Cognitive Sciences, 14(12),* 542-51. doi: 10.1016/j.tics.2010.09.008.

Plotnik, J. M., Brubaker, D. L., Dale, R., Tiller, L. N., Mumby, H. S., & Clayton, N. S. (2019). Elephants have a nose for quantity. *Proceedings of the National Academy of Sciences of the United States of America, 116 (25),* 12566-12571. doi: 10.1073/pnas.1818284116

Plotnik, J. M., Shaw, R. C., Brubaker, D. L., Tiller, L. N., & Clayton, N. S. (2014). Thinking with their trunks: Elephants use smell but not sound to locate food and exclude nonrewarding alternatives. *Animal Behaviour, 88,* 91-98. doi: 10.1016/j.anbehav.2013.11.011

Polgár, Z., Kinnunen, M., Újváry, D., Miklósi, Á., Gácsi, M. (2016). A test of canine olfactory capacity: Comparing various dog breeds and wolves in a natural detection task. *PLoS One, 11(5),* e0154087. doi: 10.1371/journal.pone.0154087

Prato-Previde, E., Marshall-Pescini, S., & Valsecchi, P. (2008). Is your choice my choice? The owners' effect on pet dogs' (*Canis lupus familiaris*) performance in a food choice task. *Animal Cognition, 11(1),* 167-174. doi : 10.1007/s10071-007-0102-7

Quignon, P., Giraud, M., Rimbault, M., Lavigne, P., Tacher, S., Morin, E., Retout, E., Valin, A., Lindblad-Toh, K., Nicolas, J., & Galibert, F. (2005). The dog and rat olfactory receptor repertoires. *Genome Biology, 6,* R83. doi: 10.1186/gb-2005-6-10-r83

Roberts, W. (2010). Distance and magnitude effects in sequential number discrimination by pigeons. *Journal of Experimental Psychology: Animal Behavior Processes, 36(2),* 206-216. doi: 10.1037/a0017226

Rouquier, S., Taviaux, S., Trask, B. J., Brand-Arpon, V., van den Engh, G., Demaille, J., & Giorgi, D. (1998). Distribution of olfactory receptor genes in the human genome. *Nature Genetics, 18,* 243-250. doi: 10.1038/ng0398-243

Rowe, C. (1999). Receiver psychology and the evolution of multicomponent signals. *Animal Behaviour, 58,* 921-931. doi: 10.1006/anbe.1999.1242

Sahibzada, N., Dean, P., & Redgrave, P. (1986). Movements resembling orientation or avoidance elicited by electrical stimulation of the superior colliculus in rats. *Journal of Neuroscience, 6(3)*, 723-733. doi: https://doi.org/10.1523/JNEUROSCI.06-03-00723.19

Steen, J. B., Mohus, I., Kvesetberg, T., & Walløe, L. (1996). Olfaction in bird dogs during hunting. *Acta Physiologica, 157(1),* 115-119. doi: 10.1046/j.1365-201X.1996.479227000.x

Theberge, J. B. & Falls, J. B. (1967). Howling as a means of communication in timber wolves. *American Zoologist, 7(2)*, 331-338. doi: 10.1093/icb/7.2.331

Ward, C. & Smuts, B. B. (2007). Quantity-based judgments in the domestic dog (*Canis lupus familiaris*). *Animal Cognition, 10(1),* 71–80. doi: 10.1007/s10071-006-0042-7

Weiss, T. F. (1966). A model of the peripheral auditory system. *Kybernetik, 3,* 153-175. doi: 10.1007/BF00290252

Wye, M. V. (2010). U.S. *Publication Number: US 2010/0095896 A1.* Washington, DC: U.S. Patent and Trademark Office.

Zozulya, S., Echeverri, F., & Nguyen, T. (2001). The human olfactory receptor repertoire. *Genome Biology, 2,* research0018.1. doi: 10.1186/gb-2001-2-6-research0018

Appendix A

Table 1

Demographics of the dogs used in each of the experiments

Dog	Age	Breed	Previous Experience	Sex	Spay/Neuter Status	Experiment(s)
Annabelle	4	English Bulldog	Y	F	N	1
Lucy	8.5	Labrador Retriever	Y	F	Y	1
Frank	3.5	English Bulldog	Y	M	N	1
Maia	5	Golden Retriever	Y	F	Y	1
Jasper	?	Whippet	?	M	?	1
Finnigan	?	Whippet	?	M	?	1
Bilbo	2	Cockapoo	Y	M	Y	1
Nutmeg	5	English Springer Spaniel	Y	F	Y	1
Cash	6	Rough Collie	Y	M	N	1
Garnett	0.21	Labrador Retriever/ Bernese Mountain Dog	N	F	N	1
Malina	13.92	West Highland Terrier	N	F	Y	2
Luna	0.25	German Shepherd/ Australian Shepherd	N	F	N	2
Sophie	9.5	Labradoodle	N	F	Y	2

Jess	5.5	Bichon Frise	N	F	Y	2
Moose	2.5	Great Pyrenees/ St. Bernard	Y	F	Y	2, 4, 5
Razz	7	Keeshond	Y	M	Y	2, 4, 5, 6
Akira	3.5	Great Pyrenees/ Maremma/Akbash	Y	F	Y	2, 4, 5
Dallas	8	Australian Shepherd	N	M	Y	2
Diesel	10	Jack Russel Terrier/ Beagle	Y	M	Y	2
Brody	8	Black and Tan Coonhound	N	M	Y	2
Blizzard	?	Husky	N	F	?	3
Indigo	0.67	Alaskan Malamute/ Husky/German Shepherd	N	F	Y	3
Athena	5	Great Dane	N	F	N	3
Luke	1	Great Pyrenees/ Bouvier des Flandres/German Shepherd	N	M	Y	3
Sophie	0.25	Great Pyrenees/ Akbash	N	F	N	3
Dante	8	Labrador Retriever	N	M	Y	3

Tioga	6	Labrador Retriever	N	F	Y	3
Henry	2.5	English Pointer	N	M	Y	3
Jorga	6	Labradoodle	N	F	Y	3, 4, 5
Jemma	5	Labrador Retriever	N	F	Y	3, 4, 5
Dean	3.58	Rough Collie Siberian Husky/ Labrador Retriever	N	M	Y	4, 5
Gus	5	Shih Tzu	N	M	Y	4, 5
Skyler	4.5	Chihuahua mix	N	F	Y	4, 5
Miley	12	Black Labrador Retriever	N	F	Y	4, 5
Maddie	2	Golden Retriever/ Labrador Retriever	N	F	N	4, 5

Note. Age is shown in years, ex. a year and a half year old dog is shown as 1.5. Previous experience and spay/neuter status are denoted Y = yes or N = no. Previous experience in experiments 1-3 refers to previous experience with any cognition study, whereas previous experience in experiments 4-6 refers to previous experience with one or more of the experiments in this study. Sex is denoted M = male or F = female. Missing data is denoted ?.

Curriculum Vitae

Name:	Shayla Jackson
Education:	Bachelor of Science (2019), Biology, Animal Behaviour University of Western Ontario, London, ON Master of Science (expected 2020), Psychology, Cognitive, Developmental and Brain Sciences University of Western Ontario, London, ON
Honours and Awards:	The Reva Gerstein Fellowship for Master's Study in Psychology (2020) Western Graduate Research Scholarship (2019) Edward Barrow and Ida Hodgins Award (2017)
Related Work Experience	Graduate Student Teaching Assignment (2020) University of Western Ontario Teaching Assistant (2019) University of Western Ontario Lab Manager in Roberts Lab (2019)
Publications:	Jackson, SM, Lo, GK, MacPherson, K, Martin, GK, Williams, WA. (2020). Information preferences across species: Pigeons, rats, and dogs. *Behav. Processes, 170:* 104016. doi: 10.1016/j.beproc.2019.104016. https://www.sciencedirect.com/science/article/pii/S0376635719304243