8-28-2018 9:00 AM

Episodic-like Memory in Dogs: Solving What-Where-When Tasks

Ka Ho Lo
The University of Western Ontario

Supervisor
Roberts, William A.
The University of Western Ontario Co-Supervisor
Sherry, David F.
The University of Western Ontario

Graduate Program in Psychology

A thesis submitted in partial fulfillment of the requirements for the degree in Master of Science

Abstract

Episodic memory is a unique, personal memory that contains *what* happened, *where* it happened, and *when* it happened. Although episodic-like memory (ELM) in non-human animals has been shown using what-where-when (WWW) memory paradigms, it has not previously been shown in dogs. Dogs are an excellent candidate for developing translational models of neurodegenerative disorders related to episodic memory, including Alzheimer's disease. Dogs were tested on experiments that involved spatially and temporally unique odour sequences. Dogs were tested to see if they remembered the odours, their locations, and their time of presentation by choosing the earlier-exposed odour at the test. Findings suggest that dogs can encode ELM, can flexibly use WWW memory on unpredictable tests, and can solve a similar what-where task without odours. My study reveals the usefulness of utilizing olfactory cues to study ELM, and its potential usefulness in examining other aspects of cognition in dogs.

Keywords

Episodic-like Memory, Episodic Memory, Dog, Canine, Cognition, What-Where-When, WWW, olfactory, olfaction, spatial

Co-Authorship Statement

All the experiments that I performed were supervised by Dr. William A. Roberts and Dr. David F. Sherry. Dr. Roberts will be co-author for future publication.

Acknowledgements

I would first like to express my sincerest gratitude to my supervisor Bill. You took me in under your wing even though I wasn't the most knowledgeable in the animal cognition field, let alone in psychology. You supported me throughout these years on not only my undergraduate and Master's work, but also on some difficult life decisions. I am forever thankful for all the opportunities you've given me.

I was very fortunate to have met now Dr. Krista Macpherson and her wonderful collies. I would not have been here had you not taken me in for volunteering opportunities, teaching me about dog cognition which I didn't even know people researched, and introducing me to Bill which have now led me here. You are a kind-hearted friend and have selflessly helped me with dog projects over and over. For that, I will always be grateful to have met you.

Thank you to Hayden MacDonald for being an amazing lab buddy. You are smart, kind, and have helped me so much around the lab when I've felt lost. I'm lucky to have you as a friend, and I wish you the best on your future endeavours. To Lyn and Austin: I wished I could have worked with you all for a longer period of time because both of you were awesome to be around. I wish you both the best. To Glynis, your enthusiasm, and your dogs, are really welcoming. I look forward to working with you in the future.

I'm very humbled to have two very respectable, smart, and kind advisors: Dr. David Sherry and Dr. Scott MacDougall-Shackleton. Thank you for taking the time out of your busy lives to help me. Your advices and suggestions for improvement have greatly helped my thesis.

I'd like to thank the dog owners. Thank you all for the friendly chats, and for allowing me to work and play with your dogs repeatedly. Thank you to all the dogs that participated in this study. I am grateful for your contributions to research. Working with each of you, with your unique personalities and quirks, kept me smiling every single day. I love you all, and will definitely give you all treats in the future.

Finally, thank you to those I love back home. To my mom, my dad, and my sister, thank you all for providing me with unfailing support. I am the person I am today because of you all, and I wouldn't be here without your encouragement throughout these years. To Alvina, thank you so much for your continuous love and support. You've helped me so much throughout the ups and downs in the past few years. You've made me a better person, and I will forever cherish our special bond.

Table of Contents

List of Tables

List of Figures

Appendix

Chapter 1

1 Introduction

1.1 Episodic-like Memory

An episodic memory is a memory of an event that one personally experienced. This experienced event involves properties that occurred during the event, including what activities occurred, where this event happened, and when this event happened in relation to other personal events (Tulving, 1972). Thus, an episodic memory is comprised of a memory for what happened which involves spatial and temporal information about the event. When an individual recalls an episodic memory, they mentally travel back in time to subjectively remember a specific event, a phenomenon known as autonoetic consciousness which was believed to be unique to humans (Tulving, 2005). However, researchers in the last two decades have revealed evidence for episodic memory in non-human animals. Animals have been shown to remember the contents of events, specifically showing that they remember "what" occurred in the past, "where" things occurred, and "when" the event happened. These what-where-when (WWW) components were deemed the behavioural criteria for episodic memory (Clayton, Bussey, & Dickinson, 2003a). Because studying these behavioural criteria cannot reveal whether non-linguistic animals have subjective autonoetic experiences, WWW memory in animals has been referred to as episodic-like memory (Clayton & Dickinson, 1998).

1.1.1 Episodic-like Memory in Non-human Animals

Episodic-like memory has now been investigated in a variety of non-human species using various WWW memory tasks. These tasks involve WWW components, and generally take advantage of animals' natural abilities or instincts. The first evidence for episodic-like memory in a non-human animal was shown in scrub jays (*Aphelocoma coerulescens*) (Clayton & Dickinson, 1998). Taking advantage of scrub jays natural food-caching behaviour, the authors showed that scrub jays could remember what types of food items they cached (a preferred perishable food item, worms, or a less-preferred non-perishable food item, peanuts), where they cached the food items, and when they cached the food items. Because their preferred food item perished naturally with time, the location at

which scrub jays should have gone to retrieve their cache depended on the amount of time elapsed between caching and retrieval. Upon a short delay between caching and retrieval (4 h), 80% of scrub jays first retrieved the preferred perishable food item. Conversely, upon a long delay between caching and retrieval (124 h), all scrub jays first retrieved the less-preferred non-perishable food item (124 h). The authors described this behaviour as only possible if the scrub jays remembered what items they cached (what), where they cached the items (where), and how long ago they cached each item (when), thus showcasing WWW memory.

Further evidence for episodic-like memory in non-human animals was shown in rats (*Rattus norvegicus*) in Babb and Crystal (2005). Taking advantage of rats' robust spatial memory on radial mazes, the authors tested rats to see if they could remember what food items they ate, where they ate these food items, and, depending on how much time passed after eating these food items, where to go to retrieve the most food items. First, rats were placed on an eight-arm radial maze, in which four of the arms were inaccessible. At the end of three accessible arms was a piece of standard rat chow, while at the end of the one remaining arm was a piece of highly preferred chocolate. Rats were then removed from the maze and returned after a period of time, in which now all eight arms were accessible. Some days rats were returned after a short interval (30 min), whereas other days rats were returned after a long interval (4 h). If rats were returned after 30 min, the previously inaccessible arms would be baited with standard rat chow and the previously visited arms would all be non-baited. If the rats were returned after 4 h, in addition to the previously inaccessible arms being baited with standard rat chow, the arm that was previously baited with chocolate was re-baited with chocolate. Optimal performance should be revisiting the chocolate arm after 4 h but not after 30 min. Rats revisited the chocolate arm more often when 4 h passed than when 30 min passed. Thus, rats, like scrub jays, can encode WWW memory by remembering what food items they visited, where they visited these items, and can make optimal decisions based on how much time has elapsed since food retrieval.

Evidence for episodic-like memory in non-human animals has been shown in various other animals. Feeney, Roberts, and Sherry (2009) showed that black-capped

chickadees (*Poecile atricapillus*), like scrub jays, choose the preferably perishable item after a short delay but not after a long delay. Similarly, Martin-Ordas, Haun, Colmenares, and Call (2010), using a task similar to that of Clayton and Dickinson (1998), showed that chimpanzees (*Pan troglodytes*), orangutans (*Pongo pygmaeus*), and bonobos (*Pan paniscus*) reliably chose the platform with a preferred perishable food after a short period of time, and reliably chose the platform with a non-perishable food after a long period of time. Thus, like scrub jays, black-capped chickadees and apes remembered what food items were located where, and chose optimally depending on how much time had passed. Additionally, Ferkin, Combs, delBarco-Trillo, Pierce, and Franklin (2008) studied episodic-like memory in meadow voles (*Microtus pennsylvanicus*) by taking advantage of their natural ability to keep track of the state of receptivity of other female voles. After one visit to a female at a certain location, male voles were able to keep track of the reproductive state of the female (what), its location (where), and make mating decisions based on how long the female will stay in its reproductive state (when). Furthermore, Pahl, Zhu, Pix, Tautz, and Zhang (2007) studied episodic-like memory in honeybees (*Apis mellifera* L.) by taking advantage of honeybees' natural foraging behaviours. Honeybees were able to forage appropriately based on what colour patterns they saw (what), which mazes they were in (where), and what time of day it was (when).

1.1.2 Elements of Episodic-like Memory

Researchers have discussed what the key elements are when developing a task to study episodic-like memory in animals. On top of the content of episodic-like memory (WWW), one other critical element of an episodic-like memory is that the structure of the memory is fully integrated (Clayton et al., 2003a). Griffiths, Dickinson, and Clayton (1999) described how a task that tests for episodic-like memory should be one in which an animal cannot make correct choices by solely remembering "what" food was cached, solely remembering "where" it cached the food, or solely remembering "when" the event occurred. Instead, an animal should only be able to perform correctly on the task by integrating all three types of WWW information components into one episodic-like memory.

Another critical element of episodic-like memory is that the memory can be used flexibly (Clayton et al., 2003a). That is, an animal should be able to change how it uses information from an encoded event based on the current conditions. Clayton, Yu, and Dickinson (2003b) showed that scrub jays demonstrated flexible expression of episodic-like memory. Scrub jays first learned to go to the proper locations to retrieve their preferred perishable food item after a short period of time but not after a long period of time. Subsequently, when the scrub jays were shown that the perishable food decayed quicker than expected, the scrub jays immediately switched their search preferences and avoided searching at the location of their now-perished food item. The authors suggested that these birds flexibly processed new information into their encoded episodic-like memory to make correct choices during food retrieval.

1.1.3 Value of Studying Episodic-like Memory in Non-human Animals

Studying episodic-like memory in non-human animals provides the opportunity to develop new translational models for neuro-degenerative diseases that affect episodic memory in humans. Alzheimer's disease, a progressive and irreversible disorder of memory and cognition, affects over 35 million people across the world (Ferri et al., 2005), and its prevalence is predicted to grow exponentially (Ballard et al., 2011; Ferri et al., 2005). Early symptoms of Alzheimer's disease typically begin with deficits in episodic memory (Bäckman, Jones, Berger, Laukka, & Small, 2004). Thus, studying episodic-like memory in animals could be a promising start to developing translational models for Alzheimer's disease.

Translational models for Alzheimer's disease have been primarily developed in mice. Mice have anatomical components highly similar to that of humans, such as hippocampal and entorhinal cortex circuits, which are impacted in patients with Alzheimer's disease (Hall & Roberson, 2012). Genetic engineering in mice is efficient and reproducible, making mice an easy-to-study model for investigating pathogenic diseases like Alzheimer's disease. Although these models have aided our understanding of Alzheimer's disease, there has been criticism of the usefulness of these models because

although they have shown promising preclinical results, they have often failed in clinical trials.

1.1.4 Episodic-like Memory in Dogs

Dogs (*Canis familiaris*) are an excellent candidate for developing a translational model for Alzheimer's disease. Unlike mice, as dogs age, they naturally undergo memory loss and decline in learning ability (Milgram, Head, Weiner, and Thomas, 1994). On a physiological level, dogs with canine cognitive dysfunction develop specific neuropathological features and inflammatory markers that correspond to those seen in humans with Alzheimer's disease (Schütt et al., 2016). Aged dogs naturally accumulate the human-type beta-amyloid in the brain, which is a peptide that is thought to lead to cognitive decline, as seen in patients with Alzheimer's disease (Hardy & Higgins, 1992). On a genetic level, the recent genetic sequencing of beta-amyloid in dogs has been shown to be approximately 98% similar to that of humans (Zerbino et al., 2018), suggesting that the processes for beta-amyloid production are similar in humans and dogs (Head et al., 2008). Furthermore, dogs naturally produce early neuropathological conditions similar to those seen in early Alzheimer's disease patients, making them an ideal model for investigating prevention of Alzheimer's disease (Davis & Head, 2014). Translational canine models have already been developed for neurogenerative diseases such as human Amyotrophic Lateral Sclerosis (ALS) (Fernández-Trapero et al., 2017), and have been said to be an optimal model due to natural genetic expressions in dogs compared to genetic modifications in rodent models (Gitler, Dhillon, & Shorter, 2017). Thus, behaviourally establishing whether dogs have episodic-like memory may be the first step for attempting to generate translational canine models of Alzheimer's disease.

The possibility that dogs encode and retrieve episodic-like memory has been suggested in a handful of studies. Fujita, Morisaki, Takaoka, Maeda, and Hori (2012) asked if dogs could solve an unexpected test based on a single past experience. In their first experiment, dogs were exposed to four open containers which were all baited with food and were allowed to eat from two of them. After 10 min, dogs were unexpectedly returned and allowed to explore the boxes; 11 out of 12 dogs first visited a container from which they had not yet eaten. In their second experiment, dogs were exposed to four

containers, two of which contained food, one of which contained an nonedible object, and one of which was empty. Dogs could explore all four containers, but could only eat from one of them. After removing the dog from the room, dogs were unexpectedly returned to the room again and made their initial visits to the container that they had not yet eaten from significantly more often than chance. The authors claimed that dogs may have incidentally encoded and retrieved "what" and "where" information from a single experience. Similarly, Fugazza, Pogány, and Miklósi (2016) asked whether dogs could rely on episodic memory to recall a certain imitated action on an unexpected test. They first trained dogs until they could imitate a specific human action on command, which involved an action at a specific location. Then, dogs were trained to lie down so that they would no longer expect to be commanded to imitate. Dogs were then unexpectedly commanded to imitate the previously trained action. Dogs were able to imitate the action after a 1-min or a 1-hr retention interval. Thus, both studies suggest that dogs have some capacity to encode a past event and recall this event to perform a proper action.

1.2 Current Study

Although dogs have been shown to remember where they did not eat (Fujita et al., 2012) and what action they previously imitated (Fugazza et al., 2016), dogs have not yet been shown to demonstrate some key elements of episodic-like memory. Dogs have not yet been shown to demonstrate the "when" component of episodic-like memory. Dogs have also not yet been shown to encode and integrate all three WWW components from personal events. Furthermore, dogs have also not yet been shown to be able to flexibly use an episodic-like memory. Thus, my current study investigates these key components by testing dogs on a WWW task.

The four experiments presented investigate if and how dogs encode episodic-like memory. In these experiments, odours were used for the "what" component, box locations were used for the "where" component, and time was used for the "when" component. Specifically, dogs were sequentially presented with four odours at four different box locations, each at a different time. Odours were used as the "what' component, as olfaction is closely linked with emotion and memory (Aggleton & Waskett, 1999; Chu & Downes, 2000; Miles & Berntsen, 2011) and has been shown to be

highly potent at evoking vivid episodic memories in humans (Adolph & Pause, 2012). In tandem with dogs' keen sense of smell (Walker et al., 2006) and impressive olfactory memory capacity (Lo, Macpherson, MacDonald, & Roberts, unpublished), olfaction serves as an ideal cue to study episodic-like memory in dogs.

Designs for Experiments 1, 2, and 3 were adapted from the WWW task used for rats by Ergorul and Eichenbaum (2004). Specifically, Experiment 1 asked if dogs could encode episodic-like memory. Dogs were first presented with a sequence of four odours (what) at four different locations (where), each at a different time (when). Then, the first odour and the last odour were presented simultaneously at the same two boxes that were visited previously. Dogs were rewarded for choosing the earlier odour in the sequence (in this case the first odour) and non-rewarded for choosing the last odour. I hypothesized that dogs would solve this WWW task by meeting a success criterion.

In Experiment 2, dogs were tested to find out if they were encoding all events from the four-event sequence, and how flexibly they could use their episodic-like memory to solve an unpredictable task. Dogs were again presented with a sequence of four odours at four different locations, each at a different time. Then, two out of the four odours were presented simultaneously at the same two boxes that were visited previously. Dogs could not predict which two would be presented. This required dogs to encode all events in the study phase and to flexibly use their memory for these events. I hypothesized that dogs would solve this WWW task by meeting a success criterion.

In Experiment 3, dogs were tested on a task which assessed whether they could encode and integrate all three WWW components in each of the four events. Dogs were again presented with the same four-event sequence as in Experiment 1 and 2. Then, dogs were tested on three different types of tests: standard tests which replicated the test used in Experiment 2, odour probe tests which removed the "where" component (box locations made irrelevant), and spatial probe tests which removed the "what" component (odours removed). If dogs only encoded "what" and "when", they should perform poorly on spatial probe tests. If dogs only encoded "where" and "when", they should perform

poorly on odour probe tests. Correct performance in all three tests required the encoding and integration of all three WWW components

Finally, in Experiment 4, dogs were tested on a similar task which completely omitted odours. This task was used to assess whether dogs could encode spatial information in the absence of olfactory information. I hypothesized that dogs would solve this where-when task by meeting a success criterion.

Chapter 2

2 Experiment 1

The objective of Experiment 1 was to investigate whether dogs have the capacity to encode episodic-like memory. A what-where-when task that involved olfaction, spatial information, and time was devised. In this task, dogs were sequentially presented with four odours that were visited at different locations and at different times. Then, dogs were simultaneously presented with the first and the last odour from the sequence. Dogs were rewarded for choosing the first odour and non-rewarded for choosing the last odour. Dogs could pass the experiment by meeting a success criterion of choosing the first odour at least five out of six times in two consecutive sessions. By placing the two previously visited odours at their previous locations, we assessed whether dogs can remember what odours they smelled, where they went to smell these odours, and when in time these events occurred. Experiment 1 served as the initial foundation test of whether dogs can demonstrate episodic-like memory by encoding what-where-when information. I hypothesized that dogs would solve this what-where-when task and thus meet the success criterion.

2.1 Methods

2.1.1 Animals

Subjects were 16 domestic dogs, *Canis familiaris*, recruited with the dog owners' permission (see Table 2.1 for age, sex, and breed of dog subjects). All dogs were experimentally naïve when beginning Experiment 1. Dogs had access to water in the testing room at all times.

2.1.2 Testing Apparatus

The testing area was an enclosed room (6.02 m X 2.77 m) with a door and windows in front and to the right of the testing apparatus. Windows were approximately 1 m off the floor. Four plastic boxes (8.5 cm x 14 cm bottom surface, 11.2 cm x 17 cm top surface, 5.4 cm in height**)** placed in a semi-circle shape were used as the testing apparatus (see

Table 2.1: Name, age, sex, and breed of dog subjects that participated in this study, ordered by age. Age was recorded by the dog owner prior to beginning Experiment 1.

Dog	**Age**	**Sex**	**Breed**
Maggie	4 months	Female	Rough Collie
Chappie	6 months	Male	German Shepherd
Bilbo	7 months	Male	Cockapoo
Frank	8 months	Male	English Bulldog
Sam	2 years	Female	German Shephard
Gus	2.5 years	Male	Maltese and Shih Tzu Mix
Sky	2.5 years	Female	Chihuahua
Annabelle	3 years	Female	English Bulldog
Maia	3 years	Female	Golden Retriever
Molly	3 years	Female	Labrador Retriever
Nutmeg	3 years	Female	English Springer Spaniel
Cash	4.5 years	Male	Rough Collie
Lucy	6 years	Female	Labrador Retriever
Sedona	6.5 years	Female	Rough Collie
Diesel	9 years	Male	Jack Russell Terrier and Beagle Mix
Soda	10.5 years	Male	Labrador Retriever

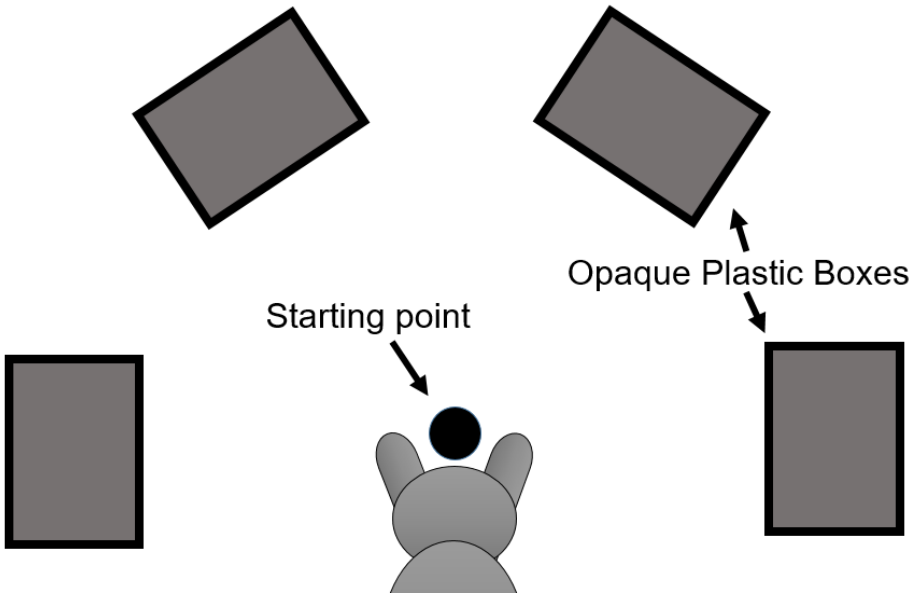

Figure 2.1: Representation of the semi-circle configuration of the testing apparatus, viewed from above. A dog image is shown in front of the starting point, illustrating where a dog would be held before making a choice during test phases. Boxes are referred to as box 1, box 2, box 3, and box 4 from left to right from the dog's perspective.

Figure 2.1). Boxes were made fully opaque using grey masking tape. The diameter of the semi-circle shape was approximately 50 cm. Adjacent boxes along the semi-circle shape were equidistant at 43 cm apart**.** Boxes were 25 cm away from the starting point which was located midway between the left end box and the right end box. Boxes were taped on the floor using grey masking tape such that the long side of the boxes faced the starting point.

To control for the possibility that dogs might choose a box based on the food reward odour, an additional plastic box was taped inside each of the four boxes attached on the floor. These additional plastic boxes were identical to the boxes attached on the floor, except that six circular holes (0.5 cm diameter) were cut out from the bottom of each box. Between the outer and inner boxes was a handful of the food reward used during testing such that dogs could smell food in all four boxes but could not access the food. Food reward varied from dog to dog based on owner recommendations, including different types of cheese, chicken sausages, and dried beef liver.

Twenty five plastic lids (11.2 cm long x 17 cm wide x 0.5 cm high) were used for the olfactory cue. The lids were made fully opaque using grey masking tape. Pieces of gauze approximately 2.5 cm long x 2.5 cm wide were taped on the centers of all 25 lids. On 24 lids, approximately one drop (5 mL) of a unique scented essential oil, supplied by the dōTERRA company located in Utah, United States, was applied on a gauze at the beginning of each testing day. Each of the lids had a different scented essential oil, for a total of 24 different essential oils based on the odours of various herbs, plants, and food odours (see Table 2.2 for a list of essential oil odours). The 24 scented lids were stored in sealed plastic bags, and were placed on a table away from the testing apparatus. The unscented lid was used for training. A white opaque tri-fold cardboard (121.9 cm x 91.4 cm) was used as a visual blocker for the dogs. Before every trial, dogs were leashed to the door handle in a way that the dog could not see the testing apparatus or the experimenter during set up. When a trial was ready to begin, dogs were removed from the door and guided around the cardboard to the testing apparatus.

Table 2.2: List of essential oil odours used in Experiments 1, 2, and 3, ordered alphabetically. Odours were obtained from the dōTERRA company.

Odours			
Arborvitae	Cypress	Lavender	Rosemary
Bergamot	Frankincense	Lime	Sandalwood
Cedarwood	Geranium	Marjoram	Spikenard
Cinnamon	Ginger	Myrrh	Tea Tree
Clary Sage	Helichrysum	Peppermint	Thyme
Cloves	Juniper Berry	Roman Chamomile	ZenGest

2.2 Procedure

2.2.1 Habituation

Before beginning Experiment 1, dogs freely explored the testing room and the testing apparatus. Dogs were given a few pieces of the food reward and were encouraged to socialize with the dog handler. The habituation phase lasted 5 to 15 min, and lid training began immediately after.

2.2.2 Lid Training

The goal of lid training was to train dogs to be comfortable with knocking over a plastic lid that fully covered a box, revealing a food reward. To do this, the handler first showed a piece of food reward to the dog before placing the food in one of the four uncovered boxes. The dog was then allowed to explore all boxes until the food was eaten. Next, the process was repeated, except after placing the food in the box, the unscented lid was immediately placed on top of the boxes covering half of the box. This was repeated until the dog comfortably knocked over the lid to obtain the food without guidance. Then, the process was repeated, except that after each successful independent food retrieval, more of the inside of the box was covered by the lid until the dog comfortably knocked over a lid that fully covered the box. Lid training was complete when the dog could knock over a fully covered lid three times. Lid training lasted around 1-10 min.

2.2.3 Testing Procedures

Dogs were tested on 1-3 sessions a day for 1-3 days a week for all experiments. For dogs that were tested for more than one session in a day, the time that elapsed between sessions ranged from 1 min to 3 h. For some dogs, their owner was present during testing and was seated near the door and out of reach of the dog. Each session contained six trials. In each trial, four unique sequential events were generated by presenting dogs with four different odours placed at different locations and at different times. Dogs were tested with two of the four odours and, critically, were rewarded for choosing the odour that was presented earlier in time in the four-odour sequence.

Specifically, each trial contained a study phase with four events and a test phase. The time that elapsed between each event in the study phase was 10-15 s, and the time that elapsed between the last event in the study phase and the test phase was 10-15 s (see Figure 2.2 for a sample trial). For the first event of the study phase, a randomly selected scented lid (for example, odour A) was placed on top of a randomly selected box that had a piece of food inside (baited). The other three boxes were empty and uncovered. The dog was then released from the door and allowed to freely explore all boxes until the lid was knocked over and the food reward was eaten. The dog would then be attached to the door handle and the scented lid would be removed from the box, ending the events. The next three study phase events were identical to the first study phase event with two crucial things involved. First, odours used for each study phase were unique within a trial, such that each trial involved four out of the 24 unique odours (for example, odour A, B, C, and D, in that order). Second, each of the four scented lids were placed on a different box, such that for every trial, one unique odour was paired with a unique location at a unique point in time over a period of approximately 1 minute. Approximately 10-15 s after the last event of the study phase, the test phase began.

In the test phase, the odours that were presented first (odour A) and last (odour D) in the study phase were placed simultaneously at the same two locations that they were placed in the study phase. Odour A was baited with food, but odour D was not. To control for the sound of baiting boxes with food as a cue, the sound of dropping the food was imitated by taping a finger on the bottom of the non-baited box. The order in which the imitated sound and the food-dropping sound were made was random, such that in some trials the imitated sound was made first, and for other trials the food-dropping sound was made first. The dog would then be guided with a leash to the starting point. The dog would be held at the starting point with a neutral grip for 5 s while the handler looked down. The dog was positioned so that the front of its body faced directly in between the two tested odours, with its front two legs behind the starting point. For example, if the two tested odours were positioned at box 1 and box 2 (see Figure 1 for specific box locations), the dog's body would face directly at the midpoint between box 1 and box 2. Before being released to make a choice, the dog was allowed to turn its head to look around or smell around, but was not allowed to move its body or touch the lids.

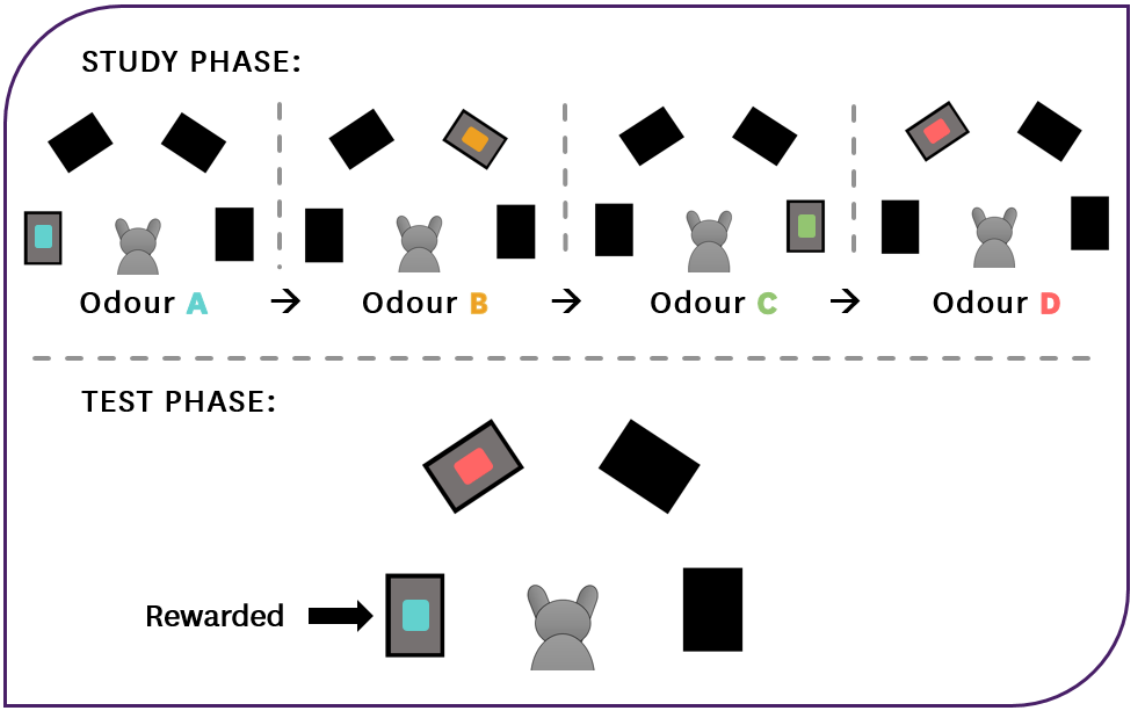

Figure 2.2: Sample trial in Experiment 1.

Upon release, a trial was deemed correct if the dog chose the earlier-visited box first (in this case, odour A). A box was considered chosen when more than 20% of the inside of the box was exposed by moving the lid. Dogs were immediately removed from the apparatus upon making an incorrect choice, except for the first session, in which they could choose the correct box following an incorrect choice to promote learning. To pass Experiment 1, dogs needed to reach a success criterion of a minimum of five out of six correct trials in two consecutive sessions (10 out of 12 consecutive trials), excluding the first session. The binomial probability of choosing correctly in 10 out of 12 trials is approximately 1.6%.

Critically, although the same 24 odours were used in every session, no sequences of four odours used for a trial were repeated for individual dogs, thus generating unique combinations of events on each trial. With 24 odours, there are over three-hundred thousand permutations of unique odour sequences. For dogs to be consistently successful, they needed to learn that the odour presented earlier in time in the study phase odour sequence was rewarded in the test phase. To do this, they needed to remember what they smelled, where they smelled it, and at what point in time these events occurred relative to each other.

2.2.4 No-food Trials

In every session, one of six trials was randomly chosen to be a no-food trial. No-food trials were identical to regular trials, except for one crucial thing: no boxes were baited. Instead, if a dog chose the correct box first, the handler would immediately toss a piece of food inside the box. It was crucial that the dog handler knew which of the two boxes was correct so that immediate reinforcement would occur upon a correct choice. No-food trials acted as an additional food control to check whether dogs would do better on regular trials than on no-food trials, possibly because they could smell which box was baited in the test phase.

2.2.5 Double-blind Testing

Because the dog handler knew which of the two tested odours was correct, human "Clever Hans" cues could have aided the dog in choosing the correct choice. To control

for this possibility, one session of double-blind testing was performed for each dog after it reached the success criterion. The procedure on this session was identical to the procedure in Experiment 1, except that two people were involved during testing. One person was responsible for setting up the study phase events, handling the dog for these events, and setting up the test phase. The other person, who faced away from the apparatus until the test phase was ready, was the dog handler for the test phases. Because the dog handler for the test phase never knew which of the two lids was correct during the testing phase, no accidental human cuing was possible. No-food trials were omitted for this test because the dog handler did not know which of the two test phase boxes were correct, making immediate reinforcement difficult.

2.3 Results

All 16 dogs reached the success criterion of five out of six correct choices in two consecutive sessions, excluding the first session. The mean number of sessions required to reach the success criterion was 5.88, $SE = 0.61$. A one sample t-test was used to assess if the mean percent correct in the last two sessions of each dog ($M = 86.98$, $SE = 1.27$) was significantly above chance (50%). Percent correct refers to the percentage of times that the dog chose the earlier-presented odour. The test revealed that dogs performance was significantly higher than chance, $t(15) = 28.20$, $p < .001$, one-tailed. A paired t-test was used to compare mean percent correct in the last two sessions with the mean percent correct of no-food trials in the last two sessions ($M = 90.63$, $SE = 5.04$). The test revealed that the difference was not significant, $t(15) = -0.72$, $p = .486$. Thus, baited trials were unlikely to have aided dogs' performance. A paired t-test was used to compare mean percent correct in the last two sessions with the mean percent correct of double-blind sessions ($M = 85.42$, $SE = 3.36$). The test revealed that the difference was not significant, $t(15) = 0.51$, $p = .617$, suggesting that potential human cuing were unlikely to have aided dogs' performance.

A learning curve averaged across dogs was plotted to examine dogs' rate of learning as sessions progressed (see Figure 2.2). The figure illustrates performance from the first session to the ninth session for all 16 dogs. Because one out of 16 dogs completed the task in 13 sessions, the percent correct in sessions 10 to 13 for that dog

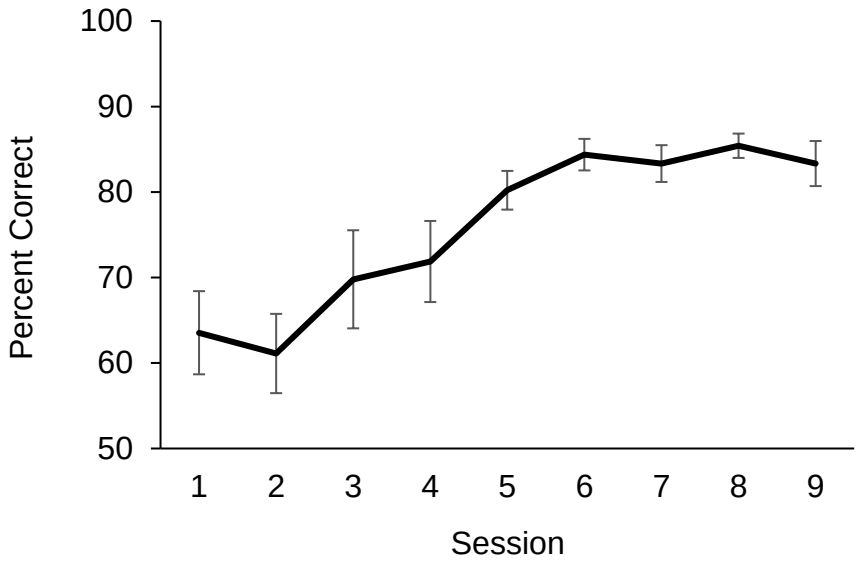

Figure 2.3: Percent correct across 9 sessions in Experiment 1. Error bars represent SEM.

were removed for illustration purposes. For dogs that reached criterion in less than nine sessions, the percent correct of their last session was repeated for all remaining sessions for illustration and statistical purposes. The curve suggests that dogs were somewhat above chance on sessions 1-2, showed a steady rise in performance to session 6, and leveled off over the subsequent sessions 7-9. A repeated measures ANOVA was performed on this curve to test for a significant increase in accuracy. Mauchly's test indicated that the assumption of sphericity had been violated, $\chi^2(35) = 102.40$, $p < .001$. As such, the degrees of freedom were corrected using Greenhouse-Geisser estimates of sphericity ($\varepsilon = .53$). The overall model revealed a significant increase in accuracy over sessions, $F(4.24, 63.54) = 6.56$, $p < .001$, $\eta_p^2 = .30$.

2.4 Discussion

Dogs completed this initial what-where-when task in just under a mean of six sessions, supporting my hypothesis for Experiment 1. There was no significant difference in performance between non-blind testing and double-blind testing, suggesting that potential human cuing were unlikely to have aided dogs' performance. There was also no significant difference between regularly baited trials and no-food trials, suggesting that dogs did not use the scent of the food reward to aid them in making choices. Figure 2.2 illustrates that dogs seem to gradually improve performance across sessions, suggesting that dogs not only learned the task, but also retained the knowledge between sessions. This observation shows impressive retention of task learning, as the time that elapsed between sessions ranged from 1 min to six weeks.

Experiment 1 provided the first line of evidence suggesting that dogs have episodic-like memory, as they could solve the what-where-when task. To solve this what-where-when task on every trial, dogs likely remembered multiple events in which they smelled different odours at different locations and at different times. They accurately recalled these events to solve the task by choosing the first visited box.

An alternative explanation that could account for the results of this experiment is that dogs may not have been remembering all four events within each trial. Instead, because the first odour out of the four-odour-sequence of each trial was always the

rewarded odour in the test phase, dogs could have learned to only remember the first odour and to ignore the rest. Similarly, because it was always the first and last odours out of the four-odour-sequence of each trial that were presented in the test phase, dogs could have learned to remember the last odour and avoided it during the test phase. In both cases, dogs could simply remember one event within a trial and ignore the other three. To assess whether dogs could remember all four events and recall these events to solve a task, dogs were tested in a second experiment in which the optimal strategy would be to remember all four events to consistently choose correctly.

Chapter 3

3 Experiment 2

The results of Experiment 1 suggested that dogs have the capacity to encode what, where, and when events occurred, and recall this episodic-like memory to solve a task. However, whether dogs were encoding all the events in the study phase and flexibly using their memory to solve the task was unclear. The objective of Experiment 2 was to determine if dogs could still solve a similar what-where-when task if it required them to remember all the events in the study phase, and if the test phase was unpredictable. Similar to Experiment 1, dogs were sequentially presented with four odours that were visited at different locations and at different times (Odour A, then B, then C, then D). Then, dogs chose from two of the four odours, which were simultaneously presented. These two odours were one of six possible odour comparisons (A vs. D, A vs. C, B vs. D, A vs. B, B vs. C, or C vs. D). Because the test phase was unpredictable, dogs needed to flexibly use their memory to solve the task each trial. Dogs were rewarded for choosing the odour that was visited earlier in the four-odour sequence, but were not rewarded for choosing the odour that was visited later in the four-odour sequence. For example, in the case of A vs. C, odour A would be rewarded and odour C would be non-rewarded. A correct choice was one in which the dog chose the rewarded odour first. Dogs could pass the experiment by meeting a success criterion of choosing the rewarded odour in five out of six trials in two consecutive sessions.

By varying odour comparisons, dogs were not able to predict which two odours from the four-odour sequence would be tested. Thus, dogs should remember all four events in the four-event sequence and flexibly use this memory in order to consistently choose correctly. I hypothesized that dogs would solve this what-where-when task and thus meet the success criterion. I also predicted that dogs would perform better at odour comparisons where the tested odours were visited further apart in time (for example, A vs. D) than odour comparisons where the tested odours were visited closer together in time (for example, C vs. D). I also predicted that dogs would demonstrate serial position effects by performing better at odour comparisons where the tested odours were

previously visited first or last (odour A or odour D) than odour pairings where the tested odours were previously visited between the first and last odours (odour B and odour C).

3.1 Methods

3.1.1 Animals

The same 16 dogs that met the success criterion in Experiment 1 participated in Experiment 2 upon completion of double-blind testing in Experiment 1.

3.1.2 Testing Apparatus

The same testing apparatus used in Experiment 1 was used in Experiment 2.

3.2 Procedure

3.2.1 Testing Procedures

The study phase used in Experiment 2 was identical to the study phase used in Experiment 1. Dogs were sequentially presented with unique odours at different locations and at different times, for a total of four unique odours per trial (odour A, then odour B, then odour C, then odour D). For the test phase, the same testing conditions used in Experiment 1 were used in Experiment 2 except for two conditions. First, one of six possible odour comparisons was tested on each trial. These comparisons included: A vs. D (the only comparison tested in Experiment 1), B vs. D, A vs. C, A vs. B, B vs. C, and C vs. D. All six comparisons were tested in a random order in each session, for a total of six trials per session. A trial was deemed correct if the dog chose the box that appeared earlier in the study phase sequence, which could involve odours A, B, or C depending on the test phase comparison. For example, if the test phase comparison was B vs. C, choosing odour B would be correct but choosing odour C would not. The second condition that differed from Experiment 1 was that dogs were immediately removed from the apparatus upon making an incorrect choice in the test phase, including the first session. This was done to keep dogs motivated to make correct choices. The same success criterion used for Experiment 1 was used for Experiment 2, which was a

minimum of five out of six correct choices in a session for two consecutive sessions, excluding the first session.

By having six possible test phase comparisons and by randomizing the order in which the comparisons were tested in each session, two conditions that encouraged episodic-like memory encoding were involved. Firstly, dogs were encouraged to encode more than one event from the study phase. If a dog used a strategy in which it only remembered the first or the last event from the study phase, the dog would not be able to meet the success criterion as there were no more than three possible comparisons that involved the first or the last odour. That is, if a dog only encoded the first event, it would not be able to perform consistently well as there were three test phase comparisons that did not involve odour A (B vs. C, B vs. D, C vs. D). Similarly, if a dog only encoded the last event, it would not be able to perform consistently well either as there were also three test phase comparisons that did not involve odour D (A vs. B, A vs. C, B vs. C).

Secondly, the test phase comparison was unpredictable. The dog could not have known which test phase comparison would appear in each trial. Although dogs could likely expect the test phase with repeated trials, they could not expect which odour comparison would be tested. As such, dogs were encouraged to flexibly use their memory of the four-event sequence. Overall, encoding all four study phase events would have been the most effective strategy to obtain the reward and thus meet the success criterion.

3.2.2 No-food Trials and Double-blind Testing

The same conditions for both the no-food trials and double-blind testing used in Experiment 1 were used in Experiment 2. That is, a no-food trial was randomly given in one of six trials every session, and a double-blind session was performed after a dog reached the success criterion. For the double-blind session, the test phase comparisons were pseudo-randomly ordered such that all six comparisons were tested once in the session.

3.3 Results

All 16 dogs reached the success criterion in a mean of 5.94 sessions, *SE* = 0.70. A one-tailed one sample t-test comparing mean percent correct of the last two sessions of each dog (*M* = 85.41, *SE* = 0.93) against chance (50%) revealed that dogs performance was significantly higher than chance, $t(15) = 37.98$, $p < .001$, one-tailed. A paired t-test was used to compare mean percent correct in the last two sessions with the mean percent correct of no-food trials in the last two sessions (*M* = 90.63, *SE* = 5.04). The test revealed that the difference was not significant, $t(15) = -1.07$, $p = .301$. Thus, baited trials were unlikely to have aided dogs performance. A paired t-test was used to compare mean percent correct in the last two sessions with the mean percent correct of double-blind sessions (*M* = 84.38, *SE* = 3.56). The test revealed that the difference was not significant, $t(15) = 0.31$, $p = .763$, suggesting that potential human cuing were unlikely to have aided dogs' performance.

A learning curve averaged across dogs was plotted to examine dogs' rate of learning as sessions progressed (see Figure 3.1). The figure illustrates performance from the first session to the tenth session for all 16 dogs. The one dog that reached criterion in 11 sessions had its eleventh session removed for illustration purposes. For dogs that reached criterion in less than 11 sessions, the percent correct of their last session was repeated for all remaining sessions for illustration and statistical purposes. The curve shows that dogs were somewhat above chance on session 1, showed a steady rise in performance to session 7, and leveled off over the subsequent sessions 8-10. A repeated measures ANOVA was performed on this curve to assess the accuracy increase. Mauchly's test indicated that the assumption of sphericity had been violated, $\chi^2(44) = 119.03$, $p < .001$. As such, the degrees of freedom were corrected using Greenhouse-Geisser estimates of sphericity ($\varepsilon = .49$). The overall model revealed a significant increase in accuracy over sessions, $F(4.41, 66.07) = 4.88$, $p = .001$, $\eta_p^2 = .25$.

The first prediction of this experiment stated that dogs would perform better at comparisons in which the tested odours were visited further apart in time than at comparisons in which the tested odours were visited closer together in time. With study phase odour presentation order defined by odour A, then B, then C, then D, the six test

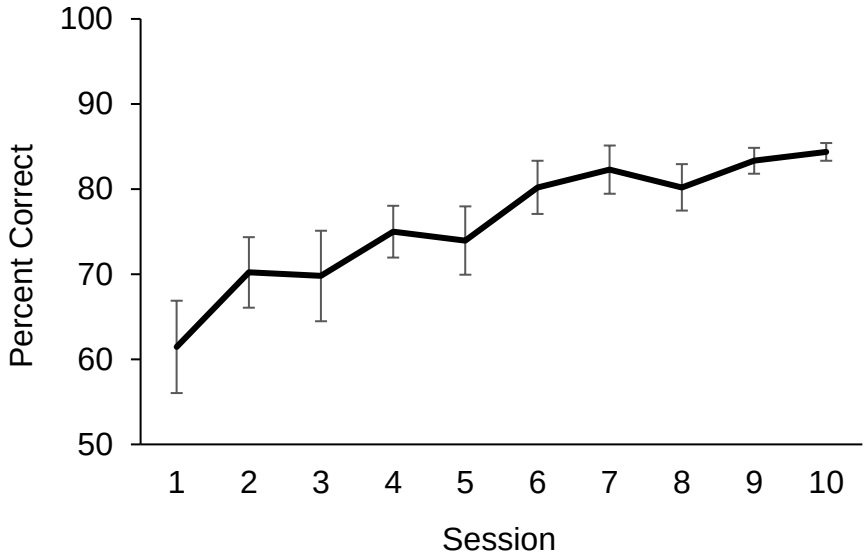

Figure 3.1: Percent correct across 10 sessions in Experiment 2. Error bars represent SEM.

phase comparisons were grouped into lag groups and shown on Figure 3.2. Comparisons were grouped by lag in the following way: lag 2 (A vs. D), lag 1 (A vs. C and B vs. D), and lag 0 (A vs. B, B vs. C, C vs. D). The lag number equals the number of odours visited in the study phase between the tested odours. For example, A vs. C is grouped into lag 1 because one odour (odour B) was visited after odour A and before odour C in the study phase. Thus, lag 2 included the test phase comparisons that had odours that were the most temporally spaced apart, lag 1 included odour comparisons that were less temporally spaced apart, and lag 0 included odour comparisons that were the least temporally spaced apart. Because the number of observations was unequal for each lag group (one comparison for lag 2, two comparisons for lag 1, and three comparisons for lag 0), scores were averaged such that there was one averaged score at each lag from each dog. For example, scores on A vs. B, B vs. C, and C vs. D were averaged as one lag 0 score for each dog. Figure 3.2 suggests that dogs performed best at lag 2, followed by lag 1, and worst at lag 0. A repeated measures ANOVA was used to assess for performance differences between lag groups. Mauchly's test indicated that the assumption of sphericity had not been violated, $\chi^2(2) = 2.52$, $p = .284$. The model revealed an overall non-significant trend in the predicted direction, $F(2, 30) = 1.72$, $p = .197$, $\eta_p^2 = .10$, with the highest percent correct at lag 2 ($M = 79.37$, $SE = 3.69$), followed by lag 1 ($M = 72.80$, $SE = 3.94$), and lowest at lag 0 ($M = 69.93$, $SE = 3.24$).

The second prediction of this Experiment stated that dogs would perform better at test phase odour pairings that were presented first or last in the study phase than odour pairings that were presented in the middle of the study phase. To test this prediction, dogs' performance at A vs. B, B vs. C, and C vs. D comparisons (lag 0 comparisons) was examined. Figure 3.3 shows accuracy at these three comparisons. By only analyzing comparisons that involved lag 0, potential lag effects were controlled. The A vs. B comparison tested for a primacy effect as it involved the first odour. Thus, if dogs show a primacy effect, they should perform best at the A vs. B comparison. Similarly, the C vs. D comparison tested for a recency effect as it involved the last odour. Thus, if dogs show a recency effect, they should perform best at the C vs. D comparison. Figure 3.3 shows that dogs performed best at the C vs. D comparison, second best at the A vs. B

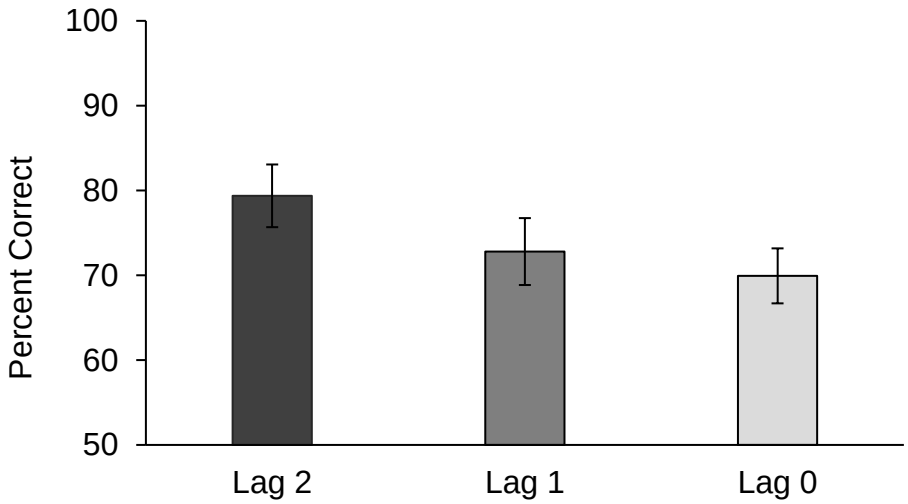

Figure 3.2: Percent correct across lag groups in Experiment 2. Error bars represent SEM.

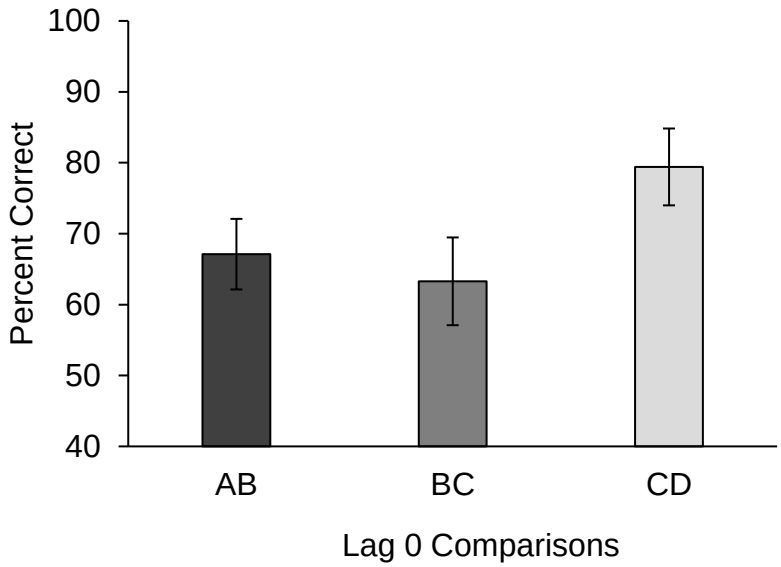

Figure 3.3: Percent correct in lag 0 comparisons in Experiment 2. Error bars represent SEM.

comparison, and slightly worse at the B vs. C comparison. A repeated measures ANOVA was used to test for performance differences between lag 0 comparisons. Mauchly's test indicated that the assumption of sphericity had not been violated, $\chi^2(2) = 3.55$, $p = .170$. The overall model was not significant, $F(2, 30) = 2.33$, $p = .114$, $\eta_p^2 = .14$. As such, there was an overall non-significant trend supporting the prediction of a serial position curve, as dogs achieved the highest percent correct at the C vs. D recency comparison (M = 79.41, SE = 5.42), followed by the A vs. B primacy comparison (M = 67.11, SE = 4.98) and the lowest at the B vs. C comparison (M = 63.28, SE = 6.19).

3.4 Discussion

All dogs met the success criterion in Experiment 2 in just under a mean of six sessions, supporting my hypothesis for Experiment 2. Similar to Experiment 1, there was no significant difference between non-blind testing and double-blind testing, suggesting that potential human cuing were unlikely to have helped dogs reach the success criterion. There was also no significant difference between regularly baited trials and no-food trials, indicating that dogs did not use the scent of the food reward to aid them in making choices. Figure 3 illustrated that dogs seem to gradually improve performance across sessions. The time that elapsed between sessions in this Experiment ranged from 1 min to four months, again showing excellent memory for the task between sessions.

Although there were no significant differences between lag conditions, the overall trend was in favour of the predicted direction. Dogs performed better at lag 2 and worst at lag 0, suggesting that it was more difficult to recall the order of odours that were less temporally separated. This result suggests that the greater the temporal separation between events (as in lag 2 comparisons), the easier it was for dogs to distinguish the events and to make correct choices. Similarly, it may be harder to distinguish the order of events that occurred closer together in time, thus explaining the poorer performance seen at lag 0 comparisons.

Although there were no significant serial position effects, the overall trend was in the predicted direction. Dogs performed better at the C vs. D comparison, which resembled the recency effect. Although dogs performed the second best at the A vs. B

primacy comparison, the difference in performance between A vs. B comparisons and B vs. C comparisons was small (M = 3.83) compared to the difference in performance between C vs. D comparisons and B vs. C comparisons (M = 12.3). Performing best at the comparison that resembled the recency effect could be explained by the fact that within each trial, less time had passed between the test phase and the previous odours C and D visits. As such, memory for more recent events may have been easier to recall than memory for events that occurred longer ago.

Overall, Experiment 2 provide an additional line of evidence supporting the idea that dogs have episodic-like memory, as they were again able to solve the current what-where-when task with unexpected tests. Because this experiment specifically required dogs to remember all the events in the study phase, the results of Experiment 2 suggested that dogs were encoding all four events in a trial. It seems highly probable that dogs remembered all four odours they smelled, where they encountered these four odours, and when in time these odours were presented.

Yet, one caveat to these results so far is that, although it seemed clear that dogs were encoding all four events in a study phase, it was uncertain as to whether dogs were encoding all three what-where-when components in these events. That is, it is possible that dogs were only encoding what odours they smelled and when they smelled them, or only encoding where they went and when they went there. Hypothetically, a dog could solely remember odours A, B, C, and D (what component) and when each of these odours was visited (when component). The dog could then have chosen correctly by strictly relying on remembering the visited odours and when in time they smelled them. Similarly, a dog could instead just remember the four box locations (where component), and remember when each of these boxes was visited (when component). The dog could have then chosen correctly by strictly relying on remembering where it visited and when in time it visited each location. To tease apart what strategies dogs were using to solve the what-where-when task, dogs were tested in a third experiment in which some tests isolated olfaction (simulating a what-when task) while other tests isolated spatial information (simulating a where-when task).

Chapter 4

4 Experiment 3

Although Experiment 2 provided strong evidence for the idea that dogs have episodic-like memory for remembering multiple what-where-when events, it was unclear whether dogs were encoding all three what-where-when components in each event. This was a crucial distinction, as a memory can only be defined as episodic-like if the what-where-when components were integrated (Clayton et al., 2003a). The objective of Experiment 3 was to investigate how dogs encoded each event to solve the what-where-when task. In this experiment, the study phase was identical to Experiment 2, as dogs were sequentially presented with four odours that were visited at different locations and at different times (Odour A, then B, then C, then D). By using the same study phase procedures, all three what-where-when components were available for encoding. Then, the six test phase comparisons were tested in three different ways.

Specifically, three different types of tests were used. The first type was identical to that of Experiment 2, which was termed the standard test. In the standard test, two odours were placed at their respective study phase locations. The second type was termed the odour probe test, in which only olfactory information was relevant. The third type was termed the spatial probe test, in which only spatial information was relevant. The results of these three tests should reveal how dogs were encoding events in the study phase. If dogs were only encoding what odours they smelled and when they were smelled (what-when components), they should perform poorly on spatial probe tests. Conversely, if dogs were only encoding the locations they went to and when they went to those locations (where-when components), they should perform poorly on odour probe tests. Correct performance on all three types of tests would suggest that dogs were encoding and integrating all three WWW components. The results of Experiment 3 will reveal how dogs encoded events to solve the what-where-when task.

4.1 Methods

4.1.1 Animals

The same 16 dogs that participated in Experiment 2 also participated in Experiment 3 upon completion of double-blind testing in Experiment 2.

4.1.2 Testing Apparatus

In addition to the apparatus used in Experiment 2, two new boxes were used, which were identical to the boxes in the original semi-circle box apparatus. These two boxes were taped down side by side at a separate location away from the original four-box apparatus within the same testing room. These boxes were 25 cm apart and were used for odour probe tests. The starting point for tests with these two boxes was in front of the boxes, 35 cm away from each box. Additionally, two new plastic opaque lids (11.2 cm long x 17 cm wide x 0.5 cm high) were used for spatial probe tests. These lids were identical to the original scented lids, except that they had no odours applied as there were no pieces of gauze attached. For tests that used this new two-box apparatus (odour probe tests), the dog would be placed so that the front of its body faced the midpoint between the two boxes (see Figure 4.1 for testing apparatus configuration of the three test phase types).

4.2 Procedure

4.2.1 Testing Procedures

The study phase used in Experiment 3 was identical to the study phase used in Experiment 2. In summary, dogs were sequentially presented with unique odours at different locations and at different times, for a total of four unique odours per trial (odour A, then odour B, then odour C, then odour D). In the test phase of a trial, one of three different test phases was used: a standard test, an odour probe test, or a spatial probe test. In the standard test, the test phase procedures were identical to the test phase procedures from Experiment 2. That is, two of the four visited odours were placed at their respective study phase locations. Dogs again were rewarded for choosing the lid that was visited earlier in the study phase sequence. Because the two test phase odours were the same two odours placed at the same two locations that they were originally placed in the study

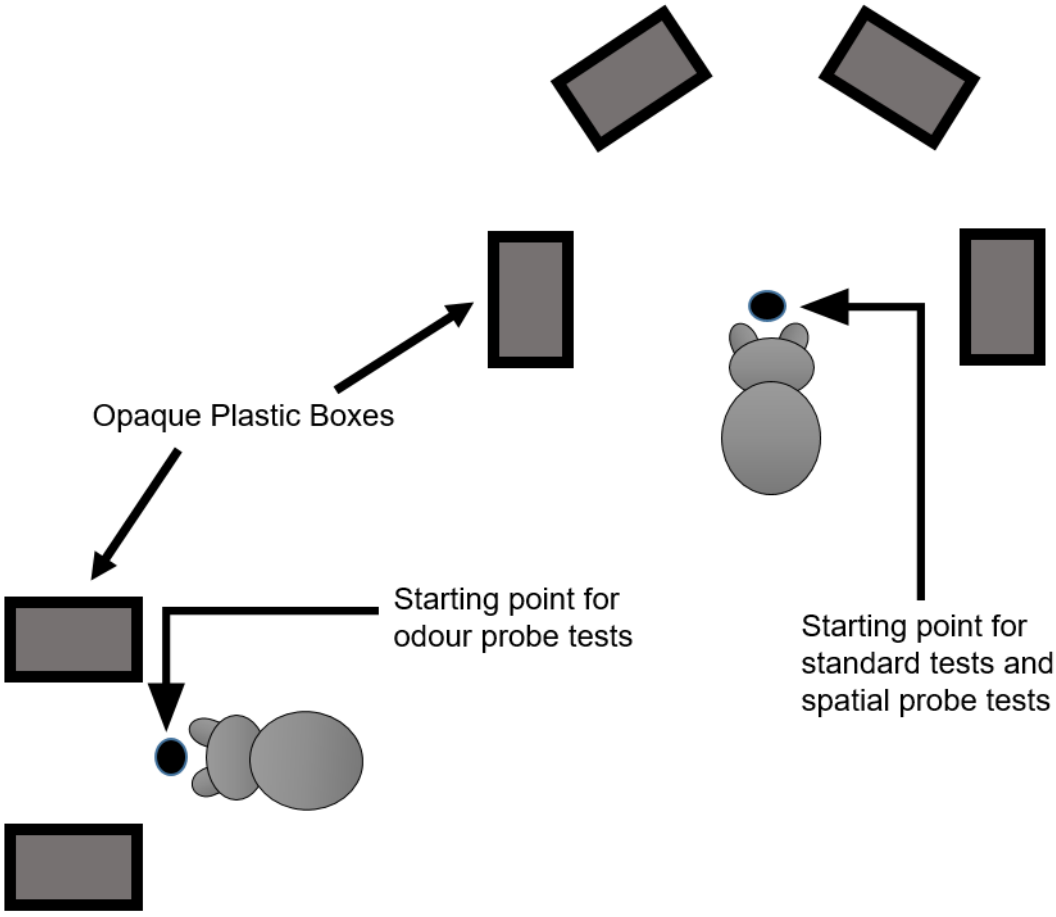

Figure 4.1: The testing apparatuses used in Experiment 3, viewed from above in the same testing room. A dog image is shown in front of both starting points, illustrating where a dog would be held before making a choice during test phases. The bottom left starting point was used for odour probe tests, and the top right starting point was used for standard tests and spatial probe tests. The four boxes in the semi-circle configuration in the top right are referred to as box 1, box 2, box 3, and box 4 from left to right from the dog's perspective. The two boxes in the bottom left are referred to as the left box and the right box from left to right from the dog's perspective.

phase, dogs could have solved this test using one of three strategies. Firstly, dog could have encoded all three what-where-when components (what odours they smelled, where they smelled these odours, and when they smelled these odours). Secondly, dogs could have encoded what odours they smelled and when they smelled these odours (what-when components). Thirdly, dogs could have encoded what locations they went to and when they went to these locations (where-when components). As such, performance at the standard test acted as a baseline to compare with performance at the odour probe tests and at the spatial probe tests. These two probe tests restricted what strategies dogs could use to be successful on the task.

In the odour probe test, dogs were also presented with two of the four odours from the study phase, except now at locations that were never visited in the study phase. Instead of placing the two odours at their positions in the four-box study phase apparatus, the two odours were placed at new two-box positions (see Figure 4.1 for details). Dogs could make a correct choice by choosing the odour that was visited earlier in the study phase sequence. Because the same two odours were presented at the test, olfactory information was relevant during this test. However, because the odours were placed at new locations that did not reflect a semi-circle configuration, spatial information was irrelevant during this test. For dogs to perform accurately on odour probe tests, they must have at least encoded olfactory information and temporal information. That is, if a dog only encoded what odours they smelled and when they smelled these odours (what-when components), the dog could still perform accurately on this task. In contrast, if a dog only encoded what locations they went to and when they went to these locations (where-when component), the dog should perform poorly on this task.

In the spatial probe test, dogs were not presented with any odours. Instead, two new odourless lids would be placed on two boxes in the same four-box semi-circle apparatus. The location of the lids depended on the order of box visits and the testing comparison. For example, if the sequence of events in the study phase was odour A at box 1, then odour B at box 2, then odour C at box 4, then odour D at box 3 (see Figure 4.1 for details on box locations), a testing comparison of B vs. D meant that the odourless lids would be placed on box 2 and box 3, and no lids would be placed on box 1 and box

4. A correct choice in this example would be box 2, the box that was visited earlier in the study phase sequence. Because the lids were placed in the same semi-circle apparatus, spatial information was relevant for this test. However, because odours were never presented in the test phase, olfactory information was irrelevant for this test. For dogs to perform accurately on spatial probe tests, they must have at least encoded spatial information and temporal information. That is, if a dog only encoded what locations they went to and when they went to these locations (where-when components), it should perform accurately on this task. In contrast, if a dog only encoded what odours it smelled and when it smelled these odours (what-when component), the dog should perform poorly on this task.

For each session, dogs were tested with two standard tests, two odour probe tests, and two spatial probe tests in a random order. Within a session, the six test phase comparisons were pseudo-randomized such that a dog would be tested with all six test phase comparisons. All dogs were tested for a total of three sessions instead of meeting a success criterion. For these three sessions, test phase comparisons were pseudo-randomized such that each dog would be tested with all six comparisons (A vs. D, B vs. D, A vs. C, A vs. B, B vs. C, and C vs. D) in each of the three different types of tests. That is, dogs were tested for a total of 18 tests, six of which were the six comparisons tested as standard tests, six of which were the six comparisons tested as odour probe tests, and the remaining six of which were the six comparisons tested as spatial probe tests.

4.2.2 No-food Trials and Double-blind Testing

A no-food trial was randomly given in one of six trials every session, and a double-blind test was performed after a dog completed all three sessions. The double-blind session would consist of 2 standard tests, two odour probe tests, and two spatial probe tests, each containing a pseudo-randomly selected test phase comparison such that all six comparisons were tested in the session. As in previous experiments, the person holding and releasing the dog was blind as to which box was the correct choice.

4.3 Results

A paired t-test was used to compare mean percent correct of all three sessions (M = 68.18, SE = 1.81) with the mean percent correct of no-food trials in all three sessions (M = 79.17, SE = 6.93). The test revealed that the difference was not significant, $t(15) = -1.69$, $p = .110$. Thus, differences observed in dogs' performance on baited and non-baited trials were not significant. A paired t-test was used to compare mean percent correct of all three sessions with the mean percent correct of double-blind sessions (M = 65.42, SE = 4.58). The test revealed that the difference was not significant, $t(15) = 0.65$, $p = .525$, suggesting that potential human cuing were unlikely to have aided dogs' performance.

Figure 4.2 illustrates dogs' performance at each lag for each of the three tests from all three sessions. For this figure, data for each dog were grouped in the following way: scores from A vs. D comparisons were grouped as lag 2, scores from B vs. D and A vs. C comparisons were averaged and grouped as lag 1, and scores from A vs. B, B vs. C, and C vs. D comparisons were averaged and grouped as lag 0. As such, the number of observations from each dog was equal at each lag. Figure 4.2 shows that dogs performed significantly above chance on all tests, except for spatial probe tests in which the tested comparison was lag 1 or lag 0. A 3 (test) by 3 (lag) repeated measures ANOVA was used to examine the effects of test (standard, odour probe, and spatial probe) and lag (lag 2, lag 1, lag 0) on task performance. Mauchly's test revealed that the assumption of sphericity was not violated for within-subjects analyses, including the analysis for test effects, $\chi^2(2) = 1.23$, $p = .540$, for lag effects, $\chi^2(2) = 0.37$, $p = .829$, and for the interaction of test and lag, $\chi^2(2) = 0.37$, $p = .829$. The ANOVA revealed a significant main effect of test, $F(2, 30) = 11.21$, $p < .001$, $\eta_p^2 = .43$, indicating that dogs performed better at some tests than at others. The ANOVA also revealed a significant main effect of lag, $F(2, 30) = 21.25$, $p < .001$, $\eta_p^2 = .59$, indicating that dogs performed better at some lags than at others. Finally, the ANOVA also revealed no significant interaction of test x lag, $F(4, 60) = 1.07$, $p = .378$, $\eta_p^2 = .07$, indicating that the main effects of test and lag acted independently on dogs' performance.

For test effects, post hoc pairwise comparisons with Bonferroni correction revealed that dogs performed significantly better at standard tests (M = 86.46, SE = 2.27)

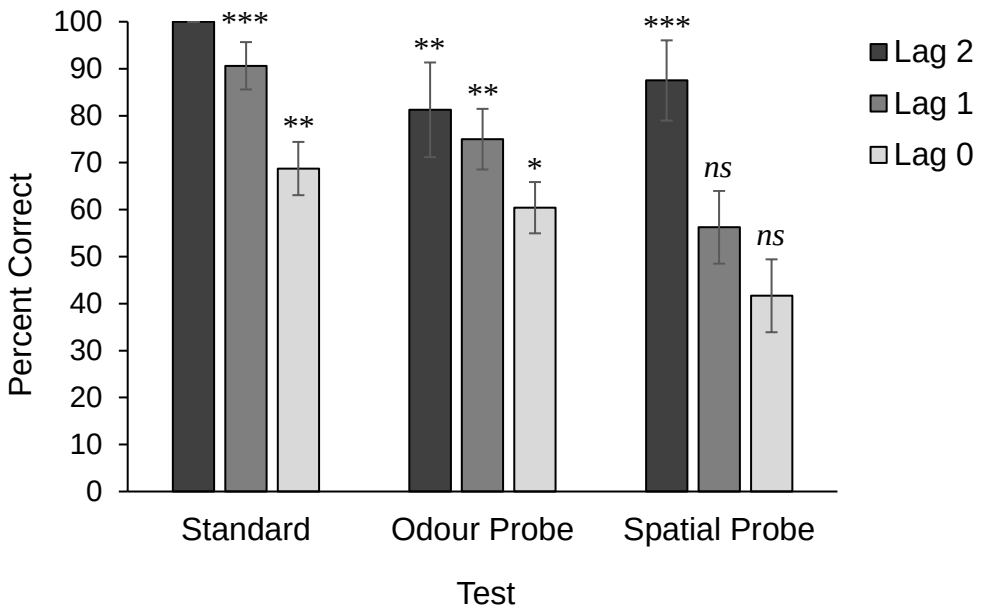

Figure 4.2: Percent correct in the three lag types across the three test types in Experiment 3. "*", "**", and "***" symbolizes scores that were significantly above chance (50%) at $p < .05$, $p < .01$, and $p < .001$, respectively. "*ns*" symbolizes scores that were not significantly different from chance. Scores from lag 2 standard tests were not analyzed due to its $SE = 0$. All p-values were obtained from one-tailed one-sample t-tests. Error bars represent SEM.

than at odour probe tests (M = 72.22, SE = 4.36), p = .024, and at spatial probe tests (M = 61.81, SE = 4.15), p = .001. No significant difference, however, was found between odour probe test performance and spatial probe test performance, p = .295. Thus, dogs performed best on standard tests. For lag effects, post-hoc pairwise comparisons with Bonferroni correction revealed that dogs performed significantly better at lag 2 (M = 89.58, SE = 3.99) than at lag 1 (M = 73.96, SE = 4.02), p = .025, and at lag 0 (M = 56.95, SE = 2.66), p < .001. Dogs also performed significantly better at lag 1 than at lag 0, p = .017. Thus, dogs performed significantly more accurately at higher lags than at lower lags.

One sample t-tests were used to assess if the mean percent correct of the three tests were significantly above chance (50%). The test revealed that dog performance was significantly higher than chance on standard tests (M = 81.25, SE = 2.99), $t(15) = 10.43$, p < .001, one tailed, significantly higher than chance on odour probe tests (M = 68.75, SE = 3.69), $t(15) = 5.09$, p < .001, one-tailed, but not significantly higher than chance on spatial probe tests (M = 54.17, SE = 4.17), $t(15) = 1.00$, p = .167, one-tailed. However, because lag effects were significant in this experiment, further analyses were performed to assess whether dogs' scores on the three tests were significantly above chance at each lag. One-sample t-tests were used to assess whether the mean percent correct of the three tests at each lag were significantly above chance. The means, standard errors, and t-test statistics are shown on Table 4.1. The test revealed that dog performance was significantly higher than chance on standard tests and odour probe tests at all three lags. Notably, dogs only performed significantly above chance on spatial probe tests when the tested comparison was lag 2. Dogs performance on spatial probe tests with lag 1 and lag 0 was not significantly different from chance.

Although initial analyses revealed that dogs did not perform significantly above chance on spatial probe tests overall, the analysis involved unequal observations for each lag group. For each test type, a dog was tested with three lag 0 comparisons (A vs. B, B vs. C, and C vs. D), two lag 1 comparisons (A vs. C and C vs. D) and only one lag 2 comparison (A vs. D). This was a crucial distinction for two reasons. Firstly, for every

Table 4.1: Dogs' performance in Experiment 3 on the three tests for each of the three lags. Mean percent correct and standard error are shown at each level, along with *t*-statistics and *p*-values obtained from one-tailed one-sample t-tests. Scores from lag 2 standard tests were not analyzed because to its $SE = 0$.

Test	Lag group	Mean Percent Correct	SE	*t*-statistic	*p*-value
Standard	Lag 2	100	0	*n/a*	*n/a*
	Lag 1	90.63	5.04	$t(15) = 8.06$	$p < .001$
	Lag 0	68.75	5.67	$t(15) = 3.31$	$p = .003$
Odour Probe	Lag 2	81.25	10.08	$t(15) = 3.10$	$p = .004$
	Lag 1	75.00	6.45	$t(15) = 3.87$	$p = .001$
	Lag 0	60.42	5.46	$t(15) = 1.91$	$p = .038$
Spatial Probe	Lag 2	87.50	8.54	$t(15) = 4.39$	$p < .001$
	Lag 1	56.25	7.74	$t(15) = 0.81$	$p = .216$
	Lag 0	41.67	7.76	$t(15) = -1.07$	$p = .150$

dog, lag 0 comparisons contributed 50% to the overall score, lag 1 comparisons contributed 33.33% to the overall score, and lag 0 comparisons contributed only 16.67% to the overall score. Because dogs performed the worst on lag 0 comparisons and the best on lag 2 comparisons, the overall score may have been lowered simply due to having more lag 0 comparisons than other lag 1 or lag 2 comparisons. To correct for unequal observations, data for each dog were initially grouped such that for each dog, there were three averaged scores for each lag at each test, rather than six ungrouped scores at each test. Then, the three averaged lag scores at each test were averaged again to obtain a single score for each test per dog. One sample t-tests were performed on these grouped scores to assess whether test scores were significantly above chance (see Table 4.2 for means, SE, and t-test statistics). The t-test revealed that dog performed significantly above chance on standard tests, odour probe tests, and notably on spatial probe tests. Thus, the at-chance performance on spatial probe tests seen with ungrouped data was likely due to unequal observations at different lags.

To test for serial position effects, dogs' performance on the three lag 0 comparisons for each test (A vs. B, B vs. C, and C vs. D) was compared. Performance at each of these comparisons is shown in Figure 4.3. Like Experiment 2, the A vs. B comparison tested for a primacy effect and the C vs. D comparison tested for a recency effect. Figure 4.3 shows that dogs were significantly better than chance at C vs. D comparisons, but no better than chance on A vs. B comparisons or on B vs. C comparisons. A repeated measures ANOVA was performed on these data to assess differences in performance between lag 0 comparisons. Mauchly's test indicated that the assumption of sphericity had not been violated, $\chi^2(2) = 2.77$, $p = .250$. The overall model was significant, $F(2, 30) = 4.826$, $p = .015$, $\eta_p^2 = .24$, suggesting that dogs performed better at some lag 0 comparisons than at other lag 0 comparisons. However, post-hoc pairwise comparisons with Bonferroni correction revealed the difference in performance at B vs. C comparisons ($M = 41.67$, $SE = 6.46$) and C vs. D comparisons ($M = 70.83$, $SE = 5.99$) was close to being significantly different, $p = .052$. Performance at A vs. B comparisons ($M = 58.33$, $SE = 5.69$) and B vs. C comparisons was also not significantly different, $p = .311$. Performance at A vs. B comparisons and C vs. D comparisons was also not significantly different, $p = .332$. Thus, the overall model showed a significant

Table 4.2: Dog performance in Experiment 3 on three test types, categorized by grouped and ungrouped data. Mean percent correct and standard error are shown for each level, along with its *t*-statistics and *p*-values obtained from one-tailed one-sample t-tests.

Test	Ungrouped/ Grouped Data	Mean Percent Correct	SE	*t*-statistic	one-tailed *p*-value against chance (50%)
Standard	Ungrouped	81.25	2.99	$t(15) = 10.43$	$p < .001$
	Grouped	86.46	2.27	$t(15) = 16.09$	$p < .001$
Odour Probe	Ungrouped	68.75	3.69	$t(15) = 5.09$	$p < .001$
	Grouped	72.22	4.36	$t(15) = 5.09$	$p < .001$
Spatial Probe	Ungrouped	54.17	4.17	$t(15) = 1.00$	$p = .167$
	Grouped	61.81	4.15	$t(15) = 2.85$	$p = .006$

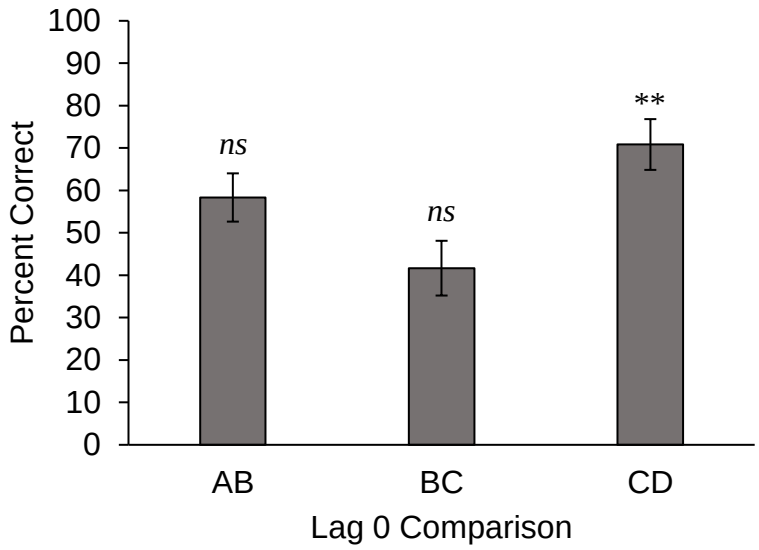

Figure 4.3: Percent correct at lag 0 comparisons in Experiment 3. "**" symbolizes scores that were significantly above chance (50%) at $p < .01$. "*ns*" symbolizes scores that were not significantly different from chance. One-sample t-tests against chance revealed t-statistics and two-tailed *p*-values for AB, BC, and CD, which were $t(15) = 1.46$, $p = .164$, $t(15) = -1.29$, $p = .216$, and $t(15) = 3.48$, $p = .003$, respectively. Error bars represent SEM.

trend in which dogs performed best at C vs. D, second best at A vs. B, and worst at C vs. D, although no two pairs of comparisons were significantly different.

4.4 Discussion

Similar to previous Experiments, there was no significant difference between non-blind testing and double-blind testing, suggesting that potential human cuing were unlikely to have helped dogs make correct choices. There was also no significant difference between regularly baited trials and no-food trials, indicating that dogs did not use the scent of the food reward to aid them in making choices.

This experiment revealed a significant effect of test, in that dogs performed significantly better at standard tests than at both odour probe tests and spatial probe tests. However, performance at odour probe tests and spatial probe tests were not significantly different. These findings suggest that dogs performed best when the test phase replicated all components available during the study phase. It is likely that when dogs encoded events in the study phase, dogs were best at remembering when events occurred (when component) if presented with all the remaining components (what and where component). That is, if a dog encoded what odours they smelled and where they smelled the odours during the study phase, the dog would remember when events occurred best (and thus choose correctly) if the odours they smelled were presented again and were presented at the same locations again.

This experiment also revealed a significant effect of lag following the same trend observed in Experiment 2, as dogs performed significantly better lag 2 than at lag 1, and significantly better at lag 1 than at lag 0. This significant finding, in addition to the same trend seen in Experiment 2, provides evidence for a temporal separation effect. That is, dogs seemed to be better at recalling the order of events when asked to compare events that occurred further apart in time than events that occurred closer together in time. Additionally, although lag 0 comparisons fell short of being significantly different from each other, the C vs. D comparison was significantly above chance. This finding is similar to the non-significant trend found in Experiment 2, in that dogs performed best at the C vs. D comparison. As such, dogs seemed to demonstrate a recency effect in which

dogs remembered events that occurred closer in time to the test than events that occurred longer ago.

Upon initial analyses of ungrouped data, dogs performed significantly above chance on standard tests, which was not surprising as the standard test procedures were identical to the test phase procedures used in Experiment 2. Interestingly, dogs performed significantly above chance on odour probe tests. As explained earlier, odour probe tests were designed such that any encoded spatial information from the study phase would not aid performance at the test, and that high accuracy on this test required the recall of at least olfactory and temporal information. Dogs' high accuracy on odour probe tests suggested that they were at least encoding what odours they smelled (what component) and when they smelled them (when component), which fulfilled two out of the three components for a what-where-when episodic-like memory.

However, initial analyses of ungrouped data revealed that dogs did not perform significantly above chance on spatial probe trials. As explained earlier, spatial probe tests were designed such that any encoded olfactory information from the study phase would not aid performance at the test, and that high accuracy on this test required the recall of at least spatial and temporal information. This finding may suggest that, although dogs were encoding the "what" and "when" components of episodic-like memory, they did not encode the "where" component. However, ungrouped data involved unequal observations for each lag. Thus, further analyses were performed, which equated the number of observations from each dog at each lag. These analyses revealed that dogs were in fact performing significantly above chance on all three tests, including spatial probe tests.

Even though dogs performed significantly better than chance on all three tests, dogs performed the worst on spatial probe tests. In fact, performance on spatial probe tests with lag 1 and lag 0 comparisons were no better than chance. Dogs' performance on spatial probe tests were only better than chance if the tested comparison was A vs. D. That is, when dogs were asked to compare where they visited first and where they visited last, they accurately recalled where they went and chose correctly. Nevertheless, this

finding suggests that dogs were encoding at least some “where” information during the study phase.

So far, the previous two experiments suggested that dogs can solve what-where-when memory tasks, and established that dogs can also encode multiple events to solve these tasks. Findings from this experiment revealed that dogs were in fact encoding all three what-where-when components in an event. Of particular interest was the spatial probe test results found in this experiment. Dogs performed significantly better than chance on spatial probe tests overall. Yet, dogs did not perform significantly better than chance on spatial probe tests with lag 1 and lag 0 comparisons. This finding suggests that lag effects were particularly relevant for dogs’ performance on spatial probe tests. Perhaps it was overall too difficult for dogs to discriminate between memories of spatial events that occurred close together in time.

There were two possible explanations as to why dogs performed poorly on spatial probe tests, but still performed significantly above chance on these tests overall. Firstly, it may be that for this task, olfactory information overshadowed spatial information. The “what” component for this task was odour, which was likely a more salient component to dogs than spatial information as dogs’ keen sense of smell is widely established (Walker, et al., 2006). When presented with the opportunity to encode both olfactory information and spatial information in the study phase, olfactory information likely overshadowed spatial information, which could have led dogs to preferentially encode more olfactory information and perform poorer on spatial probe tests.

Secondly, perhaps some trace of the odours presented in the study phase were still present near the tested boxes during the spatial probe tests. Although odours were highly concentrated onto scented gauzes on each lid, it could have been possible that odour traces from recently placed odours remained at each box location. This is possible especially because the time between the last study phase event and the test phase was short (approximately 15 s). In addition, the tested boxes in spatial probe tests were the same boxes that recently had a scented lid on them in the study phase. As such, if there

were lingering odour particles, dogs, with their keen sense of smell, may have used these odour traces to choose correctly in spatial probe tests.

To assess whether dogs relied on olfactory information to encode the “where” component for solving what-where-when tasks, dogs were tested on a final experiment that involved no odours. This final experiment was a where-when version of the same what-where-when task in which olfactory information was omitted in both the study phase and the test phase. Thus, spatial information must be encoded independently of olfactory information, and no odour traces would ever be present during the experiment. This final experiment was used to investigate whether dogs could encode the “where” component (spatial location) if the “what” component (olfaction) was unavailable for encoding.

Chapter 5

5 Experiment 4

The discussion of the previous experiment provided two possibilities that may have led to dogs' poorer performance on spatial probe tests. Olfactory information during the study phase could have led to overshadowing during encoding, or, odour traces may have been present during retrieval. As such, Experiment 4 tested dogs on a similar task in which olfactory cues were removed from both the encoding phase (study phase) and retrieval phase (test phase). This task was a where-when task, which required the dog to remember the locations they went to and when in time they went to each location. Because no olfactory information was available to the dog at any event, dogs could only rely on spatial information and temporal information to perform accurately on this task. I hypothesized that dog would be able to solve this task, and thus meet the success criterion.

5.1 Methods

5.1.1 Animals

The same 16 dogs that completed Experiment 3 also participated in Experiment 4 upon completion of double-blind testing in Experiment 3.

5.1.2 Testing Apparatus

The apparatus used in Experiment 4 was the same four-box semi-circle apparatus used in all previous experiments. In addition, three new opaque odourless plastic lids were used. These lids were identical to the odourless plastic lids used in Experiment 3. One of these lids was used only during study phases and the remaining two lids were used only during test phases. This was done to ensure that any potential olfactory cues left on the study phase lid by the dog would not be present during the test phase.

5.2 Procedure

5.2.1 Testing Procedures

The same testing procedure used in Experiment 1 was used in Experiment 4 except for one thing: scented lids were omitted, and only the three new odourless lids were used in the entire Experiment. Rather than presenting unique odours at unique locations at different times in the study phase, dogs were now presented with an odourless lid at four unique locations at different times. Specifically, in the first event of the study phase, a dog was presented with an odourless lid at one of four box locations (for example, box 4, see Figure 1 for box configuration). In the next three study phase events, the dog was presented with the same odourless lid at the three remaining box locations (for example, box 1 in the second event, box 3 in the third event, and box 2 in the fourth event). In the test phase, the dog was presented with two separate odourless lids at two locations. The position of these two new lids corresponded with the first location (baited) and last location (non-baited) that were visited in the study phase (in this case, box 4 would be baited and box 2 would not be baited). Thus, dogs could make a correct choice by choosing the first visited location. This experiment was designed with conditions that theoretically maximized performance based on findings in the previous experiment. Because those findings suggested that dogs performed best on A vs. D comparisons, only A vs. D comparisons were used on this test, similar to the procedure in Experiment 1. To pass Experiment 4, dogs needed to reach the same success criterion as that of Experiments 1 and 2, which was a minimum of five out of six correct choices in two consecutive sessions, excluding the first session.

5.2.2 No-food Trials and Double-blind Testing

A no-food trial was randomly given in one of six trials every session, and a double-blind test was performed after a dog completed all three sessions. As in previous experiments, the person holding and releasing the dog was blind as to which box was the correct choice.

5.3 Results

All 16 dogs reached the success criterion of five out of six correct choices in two consecutive sessions, excluding the first session. The mean number of sessions required to reach the success criterion was 5.13, SE = 0.68. A one sample t-test was used to determine whether the mean percent correct in the last two sessions (M = 85.41, SE = 0.93) was significantly greater than chance (50%). The test revealed that dog performance was significantly above chance, $t(15) = 37.98$, $p < .001$, one-tailed. A paired t-test was used to compare the mean percent correct in the last two sessions with the mean percent correct of no-food trials in the last two sessions (M = 90.63, SE = 5.04). The test revealed that the difference was not significant, $t(15) = -1.07$, $p = .301$. Thus, baited trials were unlikely to have aided dogs performance. A paired t-test was used to compare mean percent correct in the last two sessions with the mean percent correct of double-blind sessions (M = 80.21, SE = 3.48). The test revealed that the difference was not significant, $t(15) = 1.37$, $p = .190$, suggesting that potential human cuing were unlikely to have aided dogs' performance.

A learning curve averaged across dogs was plotted to examine dogs' rate of learning as sessions progressed (see Figure 5.1). The figure illustrates performance from the first session to the seventh session for all 16 dogs. Because three out of 16 dogs completed the task in more than seven sessions, the percent correct scores for sessions after the seventh session for these three dog were omitted for illustration purposes. For dogs that reached criterion in less than seven sessions, the percent correct of their last session was repeated for all remaining sessions for illustration and statistical purposes. The curve suggests that dogs were somewhat above chance on session 1, showed a steady rise in performance to session 5, and leveled off over the subsequent sessions 6-7. A repeated measures ANOVA was performed on this curve to test for a significant increase in accuracy. Mauchly's test indicated that the assumption of sphericity had been violated, $\chi^2(20) = 69.33$, $p < .001$. As such, the degrees of freedom were corrected using Greenhouse-Geisser estimates of sphericity ($\varepsilon = .53$). The overall model revealed a significant increase in accuracy over sessions, $F(3.20, 48.05) = 7.39$, $p < .001$, $\eta_p^2 = .33$.

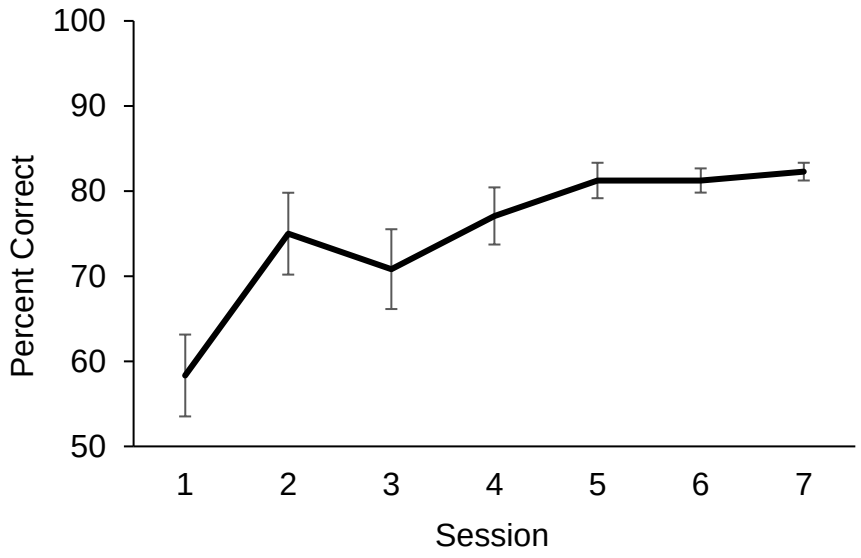

Figure 5.1: Percent correct of dogs in Experiment 4 across 7 sessions. Error bars represent standard error.

Further analyses were performed to assess whether dogs performed better in some tests than in others. Because spatial information was particularly important in this task, I investigated whether the spatial distance between the tested boxes would affect performance. That is, I compared dogs' performance between tests in which the tested boxes were close together (box 1 vs. 2, box 2 vs. 3, and box 3 vs. 4), not as close together (box 1 vs. 3 and box 2 vs. 4), and furthest apart (box 1 vs. 4). To equalize the number of observations, data were grouped into three distances (termed as "dist") and illustrated on Figure 5.2, with "dist 2" having two boxes in between the tested boxes (1 vs. 4), "dist 1" having one box in between the tested boxes (1 vs. 3 and 2 vs. 4), and "dist 0" having no boxes in between the tested boxes (box 1 vs. 2, box 2 vs. 3, and box 3 vs. 4). Figure 5.2 suggests that dogs showed slight improvement across the three distances. A repeated measures ANOVA was used to assess for significant performance differences between the three distances. Mauchly's test revealed that the assumption of sphericity had not been violated, $\chi^2(2) = 3.88$, $p = .144$. The overall model was not significant, $F(2, 30) = 0.27$, $p = .763$, $\eta_p^2 = .02$. Thus, dogs' performance on the three distances did not differ statistically

5.4 Discussion

Dogs completed this final where-when task in just over a mean of five sessions, supporting my hypothesis for Experiment 4. Like all the other three experiments, there was no significant difference between non-blind testing and blind testing and between performance on regularly baited trials and no-food trials. Thus, human cuing were unlikely to have aided dogs' performance, and the scent of the food reward were unlikely to have aided dogs' performance. Figure 5.1 illustrates that dogs gradually improved performance across sessions, as seen in Experiment 1 and 2. The time that elapsed between sessions in this Experiment ranged from 1 min to two weeks, showing strong memory for the task between sessions. Dogs did not show any significant distance effects. That is, dogs performed with similar accuracy regardless of the study phase distance between the tested boxes.

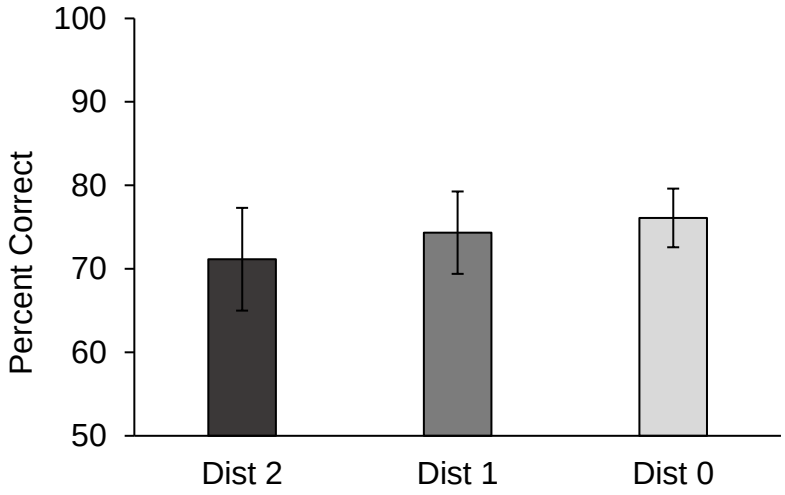

Figure 5.2: Percent correct of dogs in Experiment 4 across the three test phase distances. For the three dogs that by chance were not tested at one distance, the average score at that distance for the other dogs was used for those three dogs. Error bars represent SEM.

Overall, Experiment 4 provides evidence supporting the idea that dogs can encode the "where" component to solve a where-when task. Experiment 3 showed that although dogs performed significantly above chance on spatial probe tests (which required where-when encoding), they performed the worst on these tests. When dogs could no longer encode olfactory information, dogs were able to encode spatial and temporal information reliably to perform accurately on the test. Olfactory information may have overshadowed spatial information in Experiment 3, resulting in poorer performance on the spatial probe tests. Thus, these findings suggest that dogs were encoding all three what-where-when components to solve the what-where-when task, but likely encoded more olfactory information than spatial information.

Chapter 6

6 General Discussion

6.1 Overall Findings

The objective of the previous four experiments was to investigate whether dogs have episodic-like memory. Overall, procedures in these experiments were designed such that each event involved a “what” component, “where” component, and “when” component. These what-where-when components are the main elements of episodic-like memory, or what-where-when memory (Clayton & Dickinson, 1998; Tulving, 1972). Thus, to investigate whether dogs have episodic-like memory, dogs were tested on tasks that required the encoding and retrieval of memories for what odours were smelled at which locations and at what times. In the study phase of Experiment 1, dogs were presented with a series of unique odours at unique box locations and at different times. In the test phase, when asked to distinguish between the first visited box and the last visited box, with the first visited box always being correct, dogs met the success criterion and consistently selected the first visited box in just under a mean of six sessions of testing. This finding provided the first line of evidence suggesting that dogs used episodic-like memory to solve this initial what-where-when task. That is, they remembered each event in the study phase sequence and recalled these events accurately.

There may, however, be an alternative explanation for these findings. Because dogs were only tested with the first visited box and the last visited box, they may not have encoded all four events from the study phase. To accurately choose the first visited box, dogs may have encoded only the first event or the last event of each study phase rather than encoding all four events. Experiment 2 was designed to investigate this alternative explanation and to assess how flexibly dogs can use their encoded event memories. In Experiment 2, instead of only the first and last visited box comparison being tested, all six possible comparisons out of the four visited boxes were tested. Dogs were presented with any two out of the four odours located at their respective study phase box location. In this experiment, the box that was visited earlier in the four-box sequence was the correct choice. Dogs learned to consistently choose the earlier-visited box in just

under a mean of six sessions. It was also found that dogs trended to perform best when the temporal lag was highest and worst when the lag was lowest. That is, dogs performed best when the tested odours were visited furthest apart in time during the study phase. Because encoding one event would not result in success, findings from Experiment 2 suggest that dogs were encoding all four events from the study phase. Since the tested comparison was unexpected, correct performance in dogs suggests that they were able to flexibly use their encoded memories from the study phase. Thus, these findings provide additional evidence in support of the ability of dogs to encode episodic-like memories.

Although it was clear that dogs encoded all four events from the study phase, whether dogs were encoding all three what-where-when components of each event was still unclear. Dogs may have relied on two out of three components (either what-when or where-when) in order to consistently choose correctly in Experiment 2. Thus, dogs were tested in Experiment 3 to assess how they were encoding the events during the study phase. In Experiment 3, three types of tests were performed: standard tests (identical to Experiment 2), odour probe tests, and spatial probe tests. Accurate performance on odour probe tests meant that dogs encoded at least olfactory and temporal information, whereas accurate performance on spatial probe tests meant that dogs encoded at least spatial information and temporal information. Accurate performance on all three tests required the integration of all three what-where-when components from each event. It was observed that dogs performed significantly above chance on all three types of tests. These findings suggest that dogs encoded and integrated all three components of what-where-when memory.

Dogs' performance on Experiment 3 was, however, the worst on spatial probe tests. Despite being above chance on spatial probe tests overall, dogs' performance on spatial probe tests with lag 0 and lag 1 comparisons was no better than chance. Two explanations of the poor but above-chance performance on spatial probe tests were suggested: (1) olfactory information may have overshadowed spatial information, and (2) odour traces may have remained during test phases. To establish whether dogs could solve the task using spatial information, dogs were tested in Experiment 4 involving a where-when task that omitted odours. Accurate performance on this task required dogs to

encode spatial and temporal information. In the absence of olfactory information, dogs were still able to solve the task in just above a mean of five sessions. It was concluded that olfactory information likely overshadowed spatial information in Experiment 3. This overshadowing may have led dogs to encode more olfactory information than spatial information in Experiment 3, leading to poorer but above-chance performance on spatial probe tests.

Procedures from Experiments 1, 2, and 3 were adapted from Ergorul and Eichenbaum (2004). In their study, rats were exposed to a four-event series that consisted of four unique odours at four different locations, each at a different point in time. Just like dogs in Experiments 1 and 2, rats were able to meet a success criterion. When the rats were tested on standard tests, odour probe tests, and spatial probe tests, rats performed best on standard tests and odour probe tests, but performed no better than chance on spatial probe tests. Although rats performed no better than chance on spatial probe tests, Ergorul and Eichenbaum argued that while rats strongly relied on olfactory information to make the final correct choice, they still encoded spatial information because their initial approach was towards the correct choice at a rate significantly above chance. Similarly, although dogs performed worst on spatial probe tests in Experiment 3, dogs were able to solve the task without olfactory information in the where-when task of Experiment 4. These results suggest that dogs encode spatial information but likely encode more olfactory information when salient odours are available. Thus, both rats and dogs encoded all three what-where-when components, but olfactory information was more critical than spatial information for accurate performance. Furthermore, similar to results seen in rats in Ergorul and Eichenbaum, dogs performed better on lag 2 tests than on lag 1 and lag 0 tests. Thus, dogs were better at distinguishing between events that occurred further apart in time than events that occurred closer together in time. This result is consistent with other findings in humans and rats, which also showed better memory retrieval for events that are more temporally spaced apart than events that are less temporally spaced apart (Chiba, Kesner, and Reynolds, 1994; Madsen and Kesner, 1995).

6.2 Elements of Episodic-like Memory Revisited

Overall, dogs were able to showcase three key elements of episodic-like memory. Dogs first showcased the ability to encode the full content of episodic-like memory by solving the WWW task in Experiment 1, which involved a "what" component (odours), "where" component (box locations), and a "when" component (when in the four-event sequences). Next, dogs were able solve Experiment 2. Since Experiment 2 involved unpredictable test comparisons, dogs needed to flexibly use their encoded WWW memory from the study phase to consistently choose accurately. Finally, dogs performed optimally on all three test types in Experiment 3, which would have required the integration all three WWW components of each of the encoded events.

6.3 Serial Position Effects

Dogs' performance was similar to that of a typical serial position curve. They performed best when comparing events that occurred more recently, demonstrating a significant recency effect. Dogs did not demonstrate a primacy effect as they were no better than chance at remembering earlier events. These results are similar to those found in humans (Sands and Wright, 1980b; Healy, Havas, and Parker, 2000), rhesus monkeys (*Macaca mulatta*) (Sands and Wright, 1980a, 1980b), squirrel monkeys (*Saimiri sciureus*) (Roberts & Kraemer, 1981), rats (Roberts and Smythe, 1979), and pigeons (*Columba livia domestica*) (Shimp, 1976). In these studies, the recency effect was most prevalent, as retention for items at the end of a series was the strongest. One reason that could explain why these animals, including dogs, performed best on comparing recent items but not as well on comparing the earliest items could be the retention interval between the presented events and the test. Bolhuis and van Kampen (1988) showed that when the delay between item presentation and the test was short (30 s), only a recency effect was observed in rats. Yet, when the delay was longer (4 min or more), both the primacy effect and the recency effect were observed. This observation could explain why dogs only demonstrated the recency effect in my study, as the test phase occurred approximately 15 s after the study phase in all four experiments.

6.4 Expectedness of the Tests

Findings from my current study can also be compared with the handful of existing studies looking at episodic-like memory in dogs. Fujita et al. (2012) and Fugazza et al. (2016) showed that dogs could solve an unexpected test that require them to remember what occurred in the past. In these studies, the authors emphasized that recalling an event can only be considered an episodic memory if the event was encoded incidentally. That is, information from the event must have be encoded without knowing that it must be remembered later (Singer and Zentall, 2007; Zentall, Singer, and Stagner, 2008; Zhou, Hohmann, and Crystal, 2012). Unexpected tests were used to encourage incidental encoding, as the dogs would not have known that the event must be remembered later. This highlights a limitation of my current study, which is that dogs likely expected a test during the encoding study phase. Because dogs needed to learn that the earlier-visited box was always rewarded, repeated trials and sessions were necessary. This may have led dogs to expect a test after each study phase, thus discouraging incidental encoding. To account for this, Experiment 2 and 3 used six different comparisons during the test phase, which made it difficult for dogs to expect a specific comparison. However, dogs could have still expected a test and, regardless of test comparison, could have purposely encoded all four events from the study phase to prepare for the test phase.

6.5 Temporal Component of Episodic-like Memory

Nevertheless, the existing literature studying episodic-like memory in dogs does not address a fundamental component of episodic-like memory that my current study does: the “when” component. Although dogs have been shown to remember where they did not eat (Fujita et al., 2012) and what actions they imitated and where (Fugazza et al., 2016), dogs have not yet been shown to remember when in time these events occurred until now. The “when” component of what-where-when memory is arguably the most important yet most difficult component to document out of the three what-where-when components (Crystal, 2010). Optimal performance on all of my experiments required the encoding and retrieval of the “when” component, as dogs needed to remember when each event occurred to solve the task. Thus, my study provides the first evidence of dogs encoding all three what-where-when components of episodic-like memory.

More recently, researchers have argued about exactly what information the "when" component of episodic-like memory comprises. It has been argued that animals may not be encoding specific times as to when events occurred, but are rather encoding how long ago things occurred (Roberts et al., 2008). When events occur in a sequence, each event in the sequence will be associated with a certain trace of memory. Thus, it is possible that an animal has a sense of relative familiarity of certain aspects of events (such as how familiar an odour is compared to another odour) rather than complete recollection of the event (such as what did I smell, where did I smell it, and when). The relative familiarity strategy has been argued to be a non-episodic memory method of solving a what-where-when task as it does not involve recollection of a personal event (Crystal, 2010; Easton, Webster, and Eacott. 2012). This point highlights a limitation of my study; because events were presented sequentially, it is possible that dogs were using a relative familiarity strategy to solve the task. However, there are two aspects of my study procedures that encouraged dogs to remember specific times of each event. Firstly, the time that elapsed between events was short (15 s). This short period of time meant that the memory traces of all events were relatively similar, especially for lag 0 comparisons (15 s apart). Thus, using the strategy of relative familiarity was less relevant. Secondly, odours and the locations of boxes were used repeatedly. Specifically, all 24 odours were reused every session for Experiments 1, 2, and 3, and the same four box locations were reused every trial of every session (excluding the odour probe tests, which involved the same six box locations). According to Wright (2007), increasing item repetition not only makes a task more difficult, but can also discourage comparing the relative familiarity of events and encourage the recollection of specific memories. That is, if an animal distinguishes reused items by processing which item is more familiar than others, the animal could experience proactive interference by confusing items that were encoded this trial with items that were encoded in the previous session. This is especially relevant for my study as the time elapsed between sessions was as little as 1 min. Thus, because odours and locations were used repeatedly, correct performance from dogs in my current study suggests they were recalling specific times of each event to prevent proactive interference. Nevertheless, future research should involve a design in which

dogs could not use relative familiarity at all to solve a what-where-when task, as seen in designs used for rats in Zhou and Crystal (2009) and Panoz-Brown et al. (2018).

6.6 Concluding Statement

Overall, the findings from my study suggest that dogs can encode episodic-like memory by encoding the what-where-when aspects of multiple events and retrieving information from each event. Thus, evidence for episodic-like memory in non-human animals has again been found. Dogs not only encoded what-where-when information from each event, but also recalled these events and made flexible temporal judgements between events, even when presented with an unexpected test comparison and when a specific component was omitted during the test. Future studies should investigate dogs' ability to incidentally encode what-where-when events in which relative familiarity cues were made irrelevant. Finally, using odours to investigate episodic-like memory in dogs resulted in promising results, but has yet to be thoroughly investigated in other fields of dog cognition. Thus, odours could be a promising tool for future dog cognition research.

References

Adolph, D., & Pause, B. M. (2012). Different time course of emotion regulation towards odors and pictures: are odors more potent than pictures? *Biological Psychology, 91,* 65-73.

Aggleton, J. P., & Waskett, L. (1999). The ability of odours to serve as state-dependent cues for real-world memories: can Viking smells aid the recall of Viking experiences? *British Journal of Psychology, 90,* 1-7.

Babb, S. J., & Crystal, J. D. (2005). Discrimination of what, when, and where: implications for episodic-like memory in rats. *Learning and Motivation, 36,* 177-189.

Bäckman, L., Jones, S., Berger, A. K., Laukka, E. J., & Small, B. J. (2004). Multiple cognitive deficits during the transition to Alzheimer's disease. *Journal of Internal Medicine, 256,* 195-204.

Ballard, C., Gauthier, S., Corbett, A., Brayne, C., Aarsland, D., & Jones, E. (2011). Alzheimer's disease. *Lancet, 377,* 1019-1031.

Bolhuis, J. J., & van Kampen, H. S. (1988). Serial position curves in spatial memory of rats: primacy and recency effects. *The Quarterly Journal of Experimental Psychology, 40,* 135-149.

Chiba, A. A., Kesner, R. P., & Reynolds, A. M. (1994). Memory for spatial location as a function of temporal lag in rats: role of hippocampus and medial prefrontal cortex. *Behavioral and Neural Biology, 61,* 123-131.

Chu, S., & Downes, J. J. (2000). Odour-evoked autobiographical memories: psychological investigations of Proustian phenomena. *Chemical Senses, 25,* 111-116.

Clayton, N. S., & Dickinson, A. (1998). Episodic-like memory during cache recovery by scrub jays. *Nature, 395,* 272-274.

Clayton, N. S., Bussey, T. J., & Dickinson, A. (2003a). Can animals recall the past and plan for the future? *Nature Reviews Neuroscience, 4,* 685-691.

Clayton, N. S., Yu, K. S., & Dickinson, A. (2003b). Interacting cache memories: evidence for flexible memory use by western scrub-jays (Aphelocoma californica). *Journal of Experimental Psychology: Animal Behavior Processes, 29,* 14-22.

Crystal, J. D. (2010). Episodic-like memory in animals. *Behavioural Brain Research, 215,* 235-243.

Davis, P. R., & Head, E. (2014). Prevention approaches in a preclinical canine model of Alzheimer's disease: benefits and challenges. *Frontiers in Pharmacology, 5,* 47.

Easton, A., Webster, L. A. D., & Eacott, M. J. (2012). The episodic nature of episodic-like memories. *Learning & Memory, 19,* 146-150.

Ergorul, C., & Eichenbaum, H. (2004). The hippocampus and memory for "what," "where," and "when". (2004). *Learning & Memory, 11,* 397-405.

Feeney, M. C., Roberts, W. A., & Sherry, D. F. (2009). Memory for what, where and when in the black-capped chickadee (Poecile atricapillus). *Animal Cognition, 12,* 767-777.

Ferkin, M. H., Combs, A., delBarco-Trillo, J., Pierce, A. A., & Franklin, S. (2008). Meadow voles, Microtus pennsylvanicus, have the capacity to recall the "what", "where", and "when" of a single past event. *Animal Cognition, 11,* 147-159.

Fernández-Trapero, M., Espejo-Porras, F., Rodríguez-Cueto, C., Coates, J. R., Pérez-Díaz, C., de Lago, E., & Fernández-Ruiz, J. (2017). Upregulation of CB_2 receptors in reactive astrocytes in canine degenerative myelopathy, a disease model of amyotrophic lateral sclerosis. *Disease Models & Mechanisms, 10,* 551-558.

Ferri, C. P., Prince, M., Brayne, C., Brodaty, H., Fratiglioni, L., Ganguli, M., . . . Alzheimer's Disease International. (2005). Global prevalence of dementia: a Delphi consensus study. *Lancet, 366,* 2112-2117.

Fugazza, C., Pogány, Á., & Miklósi, Á. (2016). Recall of others' actions after incidental encoding reveals episodic-like memory in dogs. *Current Biology, 26,* 3209-3213.

Fujita, K., Morisaki, A., Takaoka, A., Maeda, T., & Hori, Y. (2012). Incidental memory in dogs (Canis familiaris): adaptive behavioral solution at an unexpected memory test. *Animal Cognition, 15,* 1055-1063.

Gitler, A. D., Dhillon, P., & Shorter, J. (2017). Neurodegenerative disease: models, mechanisms, and a new hope. *Disease Models & Mechanisms, 10,* 499-502.

Griffiths, D., Dickinson, A., & Clayton, N. S. (1999). Episodic memory: what can animals remember about their past? *Trends in Cognitive Sciences, 3,* 74-80.

Hall, A. M., & Roberson, E. D. (2012). Mouse models of Alzheimer's disease. *Brain Research Bulletin, 88,* 3-12.

Hardy, J. A., & Higgins, G. A. (1992). Alzheimer's disease: the amyloid cascade hypothesis. *Nature, 256,* 184-185.

Head, E., Pop, V., Vasilevko, V., Hill, M., Saing, T., Sarsoza, F., . . . Cribbs, D. (2008). A two-year study with fibrillar β-amyloid (Aβ) immunization in aged canines: effects on cognitive function and brain Aβ. *Journal of Neuroscience, 28,* 3555-3566.

Healy, A. F., Havas, D. A., & Parker, J. T. (2000). Comparing serial position effects in semantic and episodic memory using reconstruction of order tasks. *Journal of Memory and Language, 42,* 147-167.

Lo, K., Macpherson, K., MacDonald, H. M., & Roberts, W. A. (2018). Olfactory memory capacity and duration in dogs (Canis familiaris). Unpublished manuscript, Department of Psychology, University of Western Ontario, London, Canada.

Madsen, J. & Kesner, R. P. (1995). The temporal-distance effect in subjects with dementia of the Alzheimer type. *Alzheimer Disease & Associated Disorders, 9,* 94-100.

Martin-Ordas, G., Haun, D., Colmenares, F., & Call, J. (2010). Keeping track of time: evidence for episodic-like memory in great apes. *Animal Cognition, 13,* 331-340.

Miles, A. N., & Berntsen, D. (2011). Odour-induced mental time travel into the past and future: do odour cues retain a unique link to our distant past? *Memory, 19,* 930-940.

Milgram, N. W., Head, E., Weiner, E., & Thomas, E. (1994). Cognitive functions and aging in the dog: acquisition of nonspatial visual tasks. *Behavioral Neuroscience, 108,* 57-68.

Pahl, M., Zhu, H., Pix, W., Tautz, J., & Zhang, S. (2007). Circadian timed episodic-like memory - a bee knows what to do when, and also where. *Journal of Experimental Biology, 210,* 3559-3567.

Panoz-Brown, D., Iyer, V., Carey, L. M., Sluka, C. M., Rajic, G., Kestenman, J., . . . Crystal, J. D. (2018). Replay of episodic memories in the rat. *Current Biology, 28,* 1628-1634.e7

Roberts, W. A., & Smythe, W. E. (1979). Memory for lists of spatial events in the rat. *Learning and Motivation, 10,* 313-336.

Roberts, W. A., & Kraemer, P. J. (1981). Recognition memory for lists of visual stimuli in monkeys and humans. *Animal Learning & Behavior, 9,* 587-594.

Roberts, W. A., Feeney, M. C., MacPherson, K., Petter, M., McMillan, N., and Musolino, E. (2008). Episodic-like memory in rats: is it based on when or how long ago? *Science, 320,* 113-115.

Sands, S. F., & Wright, A. A. (1980a). Retention of serial list items by a rhesus monkey. *Science, 209,* 938-939.

Sands, S. F., & Wright, A. A. (1980b). Serial probe recognition by a rhesus monkey and a human with 10- and 20-item lists. *Journal of Experimental Psychology: Animal Behavior Processes, 6,* 386-396.

Schütt, T., Helboe, L., Pedersen, L. Ø., Waldemar, G., Berendt, M., & Pedersen, J. T. (2016). Dogs with cognitive dysfunction as a spontaneous model for early

Alzheimer's disease: a translational study of neuropathological and inflammatory markers. *Journal of Alzheimer's Disease, 52,* 433-449.

Shimp, C. P. (1976). Short-term memory in the pigeon: relative recency. *Journal of the Experimental Analysis of Behavior, 25,* 55-61.

Singer, R. A., & Zentall, T. R. (2007). Pigeons learn to answer the question "where did you just peck" and can report peck location when unexpectedly asked. *Learning & Behavior, 35,* 184-189.

Tulving, E. (1972). Episodic and semantic memory. *Organization of* Memory, *1,* 381- 403.

Tulving, E. (2005). Episodic memory and autonoesis: Uniquely human? In H. S. Terrace & J. Metcalfe (Eds), *The Missing Link in Cognition* (pp. 4-56). New York, NY: Oxford University Press.

Walker, D. B., Walker, J. C., Cavnar, P. J., Taylor, J. L., Pickel, D. H., Hall, S. B., & Saurez, J. C. (2006). Naturalistic quantification of canine olfactory sensitivity. *Applied Animal Behaviour Science, 97,* 241-254.

Wright, A. A. (2007). An experimental analysis of memory processing. *Journal of the Experimental Analysis of Behavior, 88,* 405-433.

Zentall, T. R., Singer, R. A., & Stagner, J. P. (2008). Episodic-like memory: pigeons can report location pecked when unexpectedly asked. *Behavioural Processes, 79,* 93-98.

Zerbino, D. R., Achuthan, P., Akanni, W., Amode, M. R., Barrell, D., Bhai, J., . . . Flicek, P. (2018). Ensembl 2018. *Nucleic Acids Research, 46,* D754-D761.

Zhou, W., & Crystal, J. D. (2009). Evidence for remembering when events occurred in a rodent model of episodic memory. *Proceedings of the National Academy of Sciences of the United States of America, 106,* 9525-9529.

Zhou, W., Hohmann, A. G., & Crystal, J. D. (2012). Rats answer an unexpected question after incidental encoding. *Current Biology, 22,* 1149-1153.

Appendix A

AUP Number: 2017-091
PI Name: Roberts, William
AUP Title: Studies in Dog Cognition
Approval Date: 09/01/2017

Official Notice of Animal Care Committee (ACC) Approval:
Your new Animal Use Protocol (AUP) 2017-091:1: entitled " Studies in Dog Cognition " has been APPROVED by the Animal Care Committee of the University Council on Animal Care. This approval, although valid for up to four years, is subject to annual Protocol Renewal.

Prior to commencing animal work, please review your AUP with your research team to ensure full understanding by everyone listed within this AUP.

As per your declaration within this approved AUP, you are obligated to ensure that:

1) Animals used in this research project will be cared for in alignment with:

a) Western's Senate MAPPs 7.12, 7.10, and 7.15
http://www.uwo.ca/univsec/policies_procedures/research.html

b) University Council on Animal Care Policies and related Animal Care Committee procedures

http://uwo.ca/research/services/animalethics/animal_care_and_use_policies.htm

2) As per UCAC's Animal Use Protocols Policy,

a) this AUP accurately represents intended animal use;

b) external approvals associated with this AUP, including permits and scientific/departmental peer approvals, are complete and accurate;

c) any divergence from this AUP will not be undertaken until the related Protocol Modification is approved by the ACC; and

d) AUP form submissions - Annual Protocol Renewals and Full AUP Renewals - will be submitted and attended to within timeframes outlined by the ACC.

e) http://uwo.ca/research/services/animalethics/animal_use_protocols.html

3) As per MAPP 7.10 all individuals listed within this AUP as having any hands-on animal contact will

a) be made familiar with and have direct access to this AUP;

b) complete all required CCAC mandatory training (training@uwo.ca); and

c) be overseen by me to ensure appropriate care and use of animals.

4) As per MAPP 7.15,

a) Practice will align with approved AUP elements;

b) Unrestricted access to all animal areas will be given to ACVS Veterinarians and ACC Leaders;

c) UCAC policies and related ACC procedures will be followed, including but not limited to:

i) Research Animal Procurement
ii) Animal Care and Use Records

iii) Sick Animal Response
iv) Continuing Care Visits

5) As per institutional OH&S policies, all individuals listed within this AUP who will be using or potentially exposed to
hazardous materials will have completed in advance the appropriate institutional OH&S training, facility-level training, and reviewed related (M)SDS Sheets,
http://www.uwo.ca/hr/learning/required/index.html

Submitted by: Copeman, Laura
on behalf of the Animal Care Committee
University Council on Animal Care

Dr.Timothy Regnault,
Animal Care Committee Chair

The University of Western Ontario
Animal Care
Committee / University Council on Animal Care
London, Ontario Canada N6A 5C1
519-661-
2111 x 88792 Fax 519-661-2028
auspc@uwo.ca ï¿½
http://www.uwo.ca/research/services/animalethics/index.html

Member	Primary	Secondary
Schoelier, Marianne	Yes	

Curriculum Vitae

Ka Ho (Gordon) Lo

EDUCATION

Master of Science (expected 2018), Psychology, Cognitive, Developmental and Brain Science
Western University, London, Ontario

Bachelor of Science, Honors Specialization in Biology (2017)
Western University, London, Ontario

HONOURS AND AWARDS

Western Graduate Research Scholarship (2017-2018)

RESEARCH EXPERIENCE

Research Assistant (2017-present)
Western University, London, Ontario
Supervisor: William A. Roberts, PhD

Research Volunteer (2015-2017)
Western University, London, Ontario
Primary Researcher: Krista MacPherson, PhD
Supervisor: William A. Roberts, PhD

CONFERENCES (presenting author bolded)

Lo, K., & Roberts, W. A. (2018, April). *Episodic-like memory in dogs: solving what-where-when tasks.* Poster presented at the 25th International Conference on Comparative Cognition, Melbourne Beach, FL.

Macpherson, K., Lo, K., & Roberts, W. A. (2018, April). *Olfactory memory capacity and duration in domestic dogs.* Talk given at the 25th International Conference on Comparative Cognition, Melbourne Beach, FL.

Lo, K., Macpherson, K. & Roberts, W. A. (2017, March). *Odour discrimination and memory in dogs (Canis familiaris)*. Poster presented at the 30th Ontario Biology Day, Laurentian University, Sudbury, Ontario.

PUBLICATIONS

Roberts, W. A., MacDonald, H., & **Lo, K**. (2018). Pigeons play the percentages: computation of probability in a bird. *Animal Cognition, 21,* 575-581.