Tests of olfactory memory in dogs and humans

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Abstract

Olfaction is a highly evolutionarily preserved cognitive process in the brains of animals. In the fields of psychology and neuroscience, research on olfaction has lagged far behind that of vision or other physical senses. Recent evidence suggests that decline in olfactory functioning is linked to diseases such as COVID-19, diabetes, and dementia. Outside of medical issues, dogs are relied on in societies all over the world for their olfactory abilities. Dogs serve as detection dogs trained to search for narcotics, explosives, and human remains. While advances in the study of olfaction have elucidated the neural mechanisms of olfaction, the understanding of olfaction from a cognitive perspective is also important, especially the processes governing olfactory memory. This dissertation explores methods for examining olfactory memory and the influence of proactive interference in dogs and humans. Chapter 1 is an introduction that describes recent research regarding olfaction and explains why a comparative approach is useful. Chapter 2 presents two experiments that examine how proactive interference affects dog performance in an olfactory matching task. We found that dogs perform worse on tests of olfactory memory when there is greater proactive interference as a function of repetition, as well as when the source of interference was from the immediately preceding event. Chapter 3 reports two experiments that examine human memory for olfaction. In the first experiment, participants demonstrate high accuracy for olfactory stimuli after a 30-s delay indicating memory for odors lasts at least 30 s. Participants then rated each odor in terms of intensity, verbalizability, familiarity, and pleasantness. These ratings were used to select odors for Experiment 2 by selecting odors that were all at the top of the range of ratings for each category. Experiment 2 explores how proactive and retroactive interference affect human recognition of a serially presented list of odors. Results demonstrated mixed evidence of a primacy to recency shift. These studies represent an important

step in understanding how memory processes can affect olfaction. Chapter 4 is a general conclusion that states the significance of this dissertation.

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Chapter 1: General Introduction

The chemical senses, relative to physical senses such as vision, have been relatively understudied in psychological sciences. In particular, the understanding of olfaction, including issues of sensation and perception, as well as more complex cognitive constructs such as olfactory memory, has lagged. Perhaps originally due to perceived lack of importance (i.e., olfaction is essential for survival for other animals and not humans), there has now been a relatively recent move to explore cognitive aspects of olfaction. Olfaction is important for a variety of daily tasks, such as determining whether the immediate area is safe (as in detecting a gas leak), or food is safe to eat (as in detecting rotten food). As olfactory dysfunction is increasingly shown to be an early indicator of a variety of diseases such as Parkinson's disease (Doty, 2012) and Alzheimer's disease (Choi., et al., 2018; Zou et al., 2016), as well as a symptom of diseases like diabetes mellitus (Zaghloul, et al., 2018) and COVID-19, it is clear that olfaction has great importance to human health and wellbeing and is far from a diminished sensory system more relevant to other animals. One way to advance our understanding of human olfaction is through comparisons to animal models.

Comparatively, the study of olfaction is also important. Dogs are renowned for their sense of smell and have been used by humans in a variety of roles to take advantage of this. Dogs serve as detectors of chemicals related to explosives, disease, and human remains. There is also evidence that dogs may serve as a model for human aging. While other animal models exist, dogs are unique as models of aging in that they live in the same environments as humans as companion animals, and in some cases share the same workplaces in the case of service dogs. This chapter will describe basic neuroanatomy of olfaction, as well as outline some of the open questions regarding olfaction, including the nature of olfactory perception and whether olfactory

memory systems are different than other sensory memory systems. I will also outline the reason for a comparative approach to mammalian olfaction, as well as outline the goals of this dissertation.

Neuroanatomy of olfaction

Relatively little was known about the ways in which olfactory stimuli were processed until Buck and Axel (1991) discovered that approximately 1,000 genes in the mouse genome specifically encode the olfactory receptors (OR) in the mouse. This lead to the "one gene, one receptor" hypothesis (Bystrova & Kolesnikov, 2021; Mombaerts, 2004), which suggests each of the 1,000 genes for olfactory receptors in the rat genome, and the approximately 350 in the human genome, each express a single OR, which in turn determines chemical sensitivity for the olfactory sensory neuron (OSN) it is attached to. To contrast with vision, there are three types of receptors in the human eye that give rise to color vision, one each for blue, green, and red. Put another way, 1,000 of the 30,000 genes in the mouse genome are dedicated to olfactory receptors (Mackay-Sim & Royet, 2006). Olfaction is unique in the way it processes stimuli. OSNs are embedded in the olfactory mucosa, which covers the superior, posterior area of the nasal cavity. The axons from a particular OSN form bundles with other axons of similar sensitivity. These bundles synapse onto olfactory glomeruli on the surface of the olfactory bulb (OB). The OB maintains the zoning of the olfactory epithelium, such that all axon bundles from one area of the epithelium are also kept in a corresponding region on the OB (Mackay-Sim & Royet, 2006). It appears that each OB region receives afferent information from OSNs that respond to different chemicals with the same or similar functional groups (Johnson, et al., 2002). Chemicals in the same functional group can be differentiated from each other via carbon chain length (Leon & Johnson, 2003). That is, two different odors can have an acidic functional group and different

carbon chain lengths, and thus be discriminated as different odors. These different odors would also be represented by different glomeruli in the olfactory bulb, but these glomeruli would be in the same zone. Location in the zone is dependent on carbon chain length, so two odors with similar length will be represented by glomeruli that are closer together than two odors with very different lengths. After processing in the OB, olfactory information is transferred to the piriform cortex. From there, olfactory information is moved to the thalamus, which is the opposite order of other sensory systems such as vision (Zhou et al., 2019), which sends information to the thalamus before it reaches the visual cortex. This different route is unique to olfaction and may lead to processing differences that may be evident in cognitive tasks. Final processing takes place in the orbitofrontal cortex (Watanabe et al., 2018), where olfactory information is integrated with other sensory information (Rolls et al., 1996).

Olfactory perception and memory

The progress made in detailing the specific pathways of OSNs and OB glomeruli has perhaps lead to the expectation that researchers can predict the perception of an odor based on its chemical structure (i.e., analytically). This does not seem to be the case, or at least is not easily done. Figure 1.1, from Sell (2006) shows how chemicals with different structures can produce similarly perceived scents, while chemicals with similar structures can produce different scents. As one changes the chemical structure of an odorant, there is not necessarily a predictable change in percept. This issue can be traced to OSN sensitivity, where some OSNs are sensitive to a variety of odors and a single odor can be detected by several OSNs simultaneously. Complete understanding of the olfactory system cannot come from anatomical studies of the OB alone. For example, while one may be able to identify the categorical differences of smells according to functional group (whether the odor is alcoholic), there does not seem to be a common change in

the recognition of an odor based on changes to carbon chain length. The perception of odor mixtures supports this. A cup of coffee has a distinct, recognizable smell, yet is the product of many chemicals and odorants. The smell of a rose is similarly composed of many different chemical components. Despite this, coffee and roses are perceived holistically. The same could be said of a stew, where one might have placed different vegetables, spices, and meats into a pot that has been cooked for several hours. Eventually, it smells like stew and not the individual components. At some point, these mixtures of odors come to be detected as single unitary smell. It is estimated that the human olfactory system can discriminate over 1 trillion olfactory stimuli, including mixtures (Bushdid et al., 2014), as most OSNs respond to more than one odor (Schlief & Wilson, 2007). While more is known about the way the olfactory system processes monomolecular smells (Thomas-Danguin et al., 2014), less is known about olfactory processing and perception of odor mixtures, partially because once again, in blending odors it is difficult to predict which odors will dominate the perception of the mixture, and which will blend together to create a new percept.

Wilson and Stevenson (2003) propose a synthetic approach to olfaction, where experience and expectations cause top-down effects on the identification and recognition of odors. Figure 1.2 is a depiction of this account, and shows how information from associative areas (e.g., orbital frontal cortex,) can assert influence during the encoding of stimuli, affecting perception and identification. Rather than trying to extricate top-down effects from studies of perception in order to find underlying processes (e.g., reduce olfaction to analytic chemistry), Wilson and Stevenson argue that it is most important to look at how cortical layers encode complex olfactory information as olfactory objects, replete with expectations and memories regarding these objects. To make sense of 1 trillion different possible combinations of odors,

many of which bear no direct evolutionary importance (e.g., the smell of plastic), the olfactory system, especially that of mammals, has mechanisms for responding to both highly stereotyped odors with evolutionary relevance, as well as novel creations that an animal's ancestors never would have encountered (Wilson and Stevenson, 2006). This theory asserts that perceptual stimulus learning and resultant memories are necessary for discriminating odors (Wilson & Stevenson, 2003), especially in the context of odor mixtures, citing evidence that suggests human participants show worse discrimination accuracy when identifying individual components of mixtures, especially when they were unfamiliar (Rabin, 1988), and that experts are only marginally better at detecting odors in a mixture (up to a certain point; Livermore & Laing, 1996). Understanding the nature of olfactory memory would be, in this view, necessary for understanding the olfactory system itself.

Investigations of olfactory memory in humans are often confounded with other sensory systems. For example, if one were tasked with recalling a recently smelled odor, one does not necessarily have to use a reference memory of the odor itself. The experience of smelling that odor will also be encoded with a verbal label of that odor and perhaps even a visual representation of that object (i.e., smelling an apple might be encoded as the word *apple*, and the visual representation of an apple). Preventing the use of verbal labels, such as by using hard-to-name or unfamiliar odors, can reduce the influence of verbal codes on olfaction. There may be a separate olfactory specific working memory store (Zelano et al., 2009), which may or may not follow rules of memory similar to other senses. Isolating this system from redundant coding (i.e., a single item may be coded by its color, as well as its shape, feel, label, etc.) is a difficult, yet vital goal; separating olfactory memory processes from redundant coding by other sensory apparatuses is a relevant pursuit in understanding olfaction as these redundant codes can create a

lack of clarity in studies that do not control for verbal codes. The difficulty in controlling for other, redundant memory stores is less of an issue with nonhuman animals (hereafter animals). While there is evidence that dogs, for example, maintain cross-modal representations of objects that include visual and olfactory information (Bräuer & Belger, 2018; Bräuer & Blasi, 2021), the issue of verbal labels can be more easily mitigated by studying animals.

Comparative approach

First, much of what has been learned already uses a comparative approach. The Buck and Axel (1991) study that found that each gene expresses a single OSN, for which they won a Nobel Prize in medicine, informed our understanding of human olfaction despite using mice as subjects. Olfaction represents an evolutionarily ancient system of sensation and perception, one that is highly persevered not just amongst mammals but among all vertebrates as well. Similar processes are seen in insects, representing evolutionary convergence (Imai, 2000). Comparisons between species, especially mammals, can help clarify necessary components of the olfactory system, as all mammals share similar olfactory structures with this in mind, the idea that humans might have such a limited or diminished olfactory system that it cannot be separated from verbal labels is unlikely. Comparative studies can elucidate the cognitive processes, sans language, that are necessary to olfactory perception.

Dogs are particularly interesting as a comparative subject for many reasons. One, like rodents, they have evolved an olfactory system that, while made of the same components of the human olfactory system, is more robust, with more active OR genes (Quignon, 2003). They are thus valued in human societies all over the world as service animals. For example, dogs are used to detect narcotics, explosives (Furton et al., 2001), and human remains (Riezzo et al., 2014). In some areas they are used to match scents of suspects to scents collected from a crime scene

(Ferry et al., 2019). Dogs can even be used in conservation work to find endangered animals (Beebe et al., 2016). They have also proven adept at detecting various diseases, from cancers to viral infections (Taverna et al., 2015). There is a great deal of interest in exploring the cognitive processes of dogs as they relate to olfaction for these reasons. Training dogs to serve these roles is costly to trainers and agencies that employ them, but also not of insignificant cost to dogs as well. Better understanding of these processes can help to improve the efficiency of dog training and selection for these roles, as well as ensure humane treatment of all animals (Cobb et al., 2015).

Understanding olfaction and cognition in dogs has another important benefit: translational research. Dogs have been increasingly identified as a model for human aging. Older dogs can suffer from canine cognitive dysfunction (CCD), a disease that appears similar in etiology to Alzheimer's disease in humans (Urfer, et al., 2021). Dogs, unlike other animal models of AD such as mice, develop amyloid beta plaques, which seem to be implicated in the progression of AD in humans. Urfer et al. (2021) found that, similar to humans, increasing rates of amyloid beta buildup in the prefrontal, temporal, entorhinal cortices in companion dogs was correlated with CCD scale scores. The use of companion dogs here demonstrates another benefit of using dogs as a model of aging: that companion dogs spend many years of their lives in the exact same environments as their owners do. This could better allow for understanding potential environmental influences on the development of AD. Pet dogs are also genetically diverse in a way that laboratory mice (as genetic clones) are not, which would allow the identification of genes that predispose or protect against AD.

Dissertation Outline

This dissertation discusses two studies that further examine olfactory memory. These studies were designed to explore issues related to interference and olfaction, a relatively unknown aspect of olfactory memory (Moss et al., 2016). In Chapter 2, I outline two experiments with detection dogs. These experiments explore the effects of proactive interference in the context of olfactory recognition memory in dogs. Proactive interference (PI) occurs when memories for items occurring earlier in time cause confusion about items or events that occurred later. This can be assessed in recognition tests, where PI from items that occurred earlier (e.g., a stimulus that is currently a distractor was previously a target) cause worse recognition at the time of test. In Chapter 3, I report a study to explore both proactive and retroactive interference (RI; where memory of a more recent item impedes memory for an earlier item) in the context of list memory using human participants. Establishing an olfactory serial position function (SPF) in humans is a useful first step in developing these tests for dogs. Chapter 4 provides a general conclusion to the dissertation.

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Figure 1.1

From Sell, 2006. This demonstrates that the odor percept (in parentheses) can be similar for different molecules, as well as different for similar molecules.

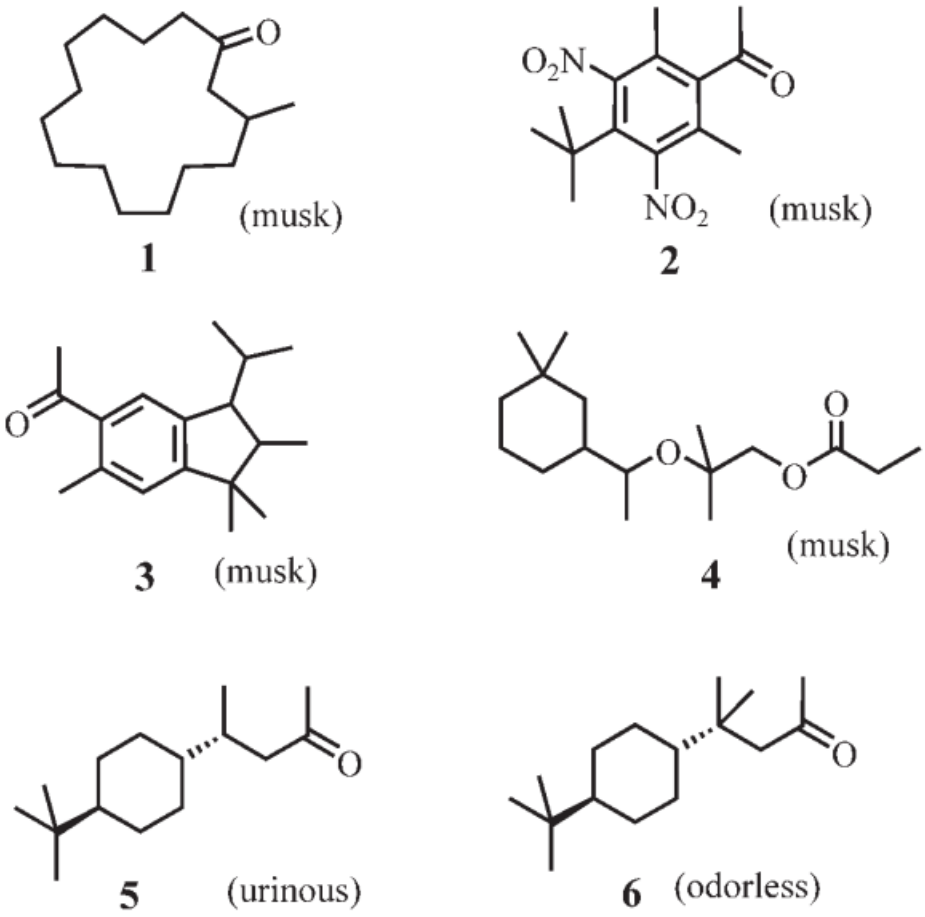
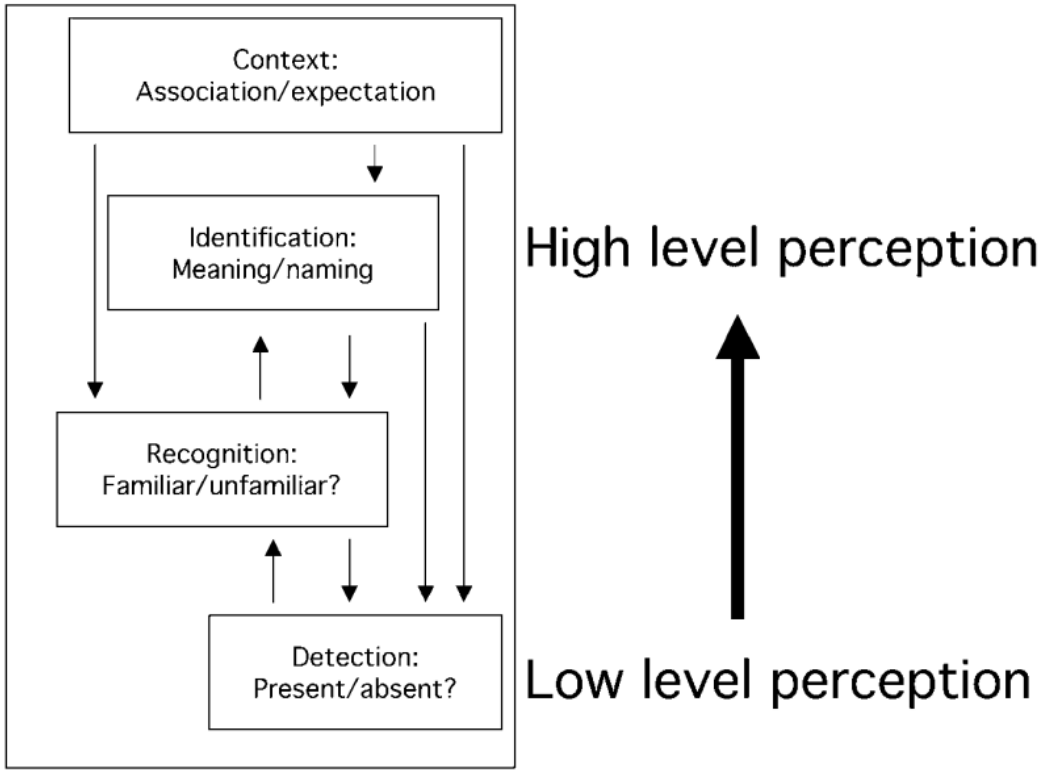


Figure 1. Different molecules, similar odors; and vice versa.

Figure 1.2

From Wilson and Stevenson, 2006. This is a diagram suggesting memories of associations and expectations affects all levels of olfactory perception.



Chapter 2: Effects of proactive interference on olfactory memory in dogs

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Abstract

Proactive interference (PI) occurs when memories of past events or stimuli intrude in the present moment, causing working memory (WM) errors. These errors are often measured through WM tests such as matching-to-sample (MTS). When the repetition of individual stimuli increases, there is a greater chance of these intrusions, and thus there can be a decrease in accuracy in such tasks. In two experiments, we explored the nature of PI on dog working memory. First, we manipulated the size of the set of odors (2, 6, trial-unique) used to construct each session to maximize (2-odor set) and minimize (trial-unique) within-session proactive interference during an olfactory MTS task. Matching-to-sample accuracy decreased with greater PI. Second, we adapted procedures originally designed for pigeons and rhesus macaques to determine the locus of PI in dogs. To test for proactive interference, probe trials were inserted into MTS sessions where sample odors from earlier trials reappeared as incorrect comparisons. Incorrect responses on these probe trials indicated proactive interference. These probe tests were conducted with a 0 s or 20 s retention interval in separate sessions. We found that dogs performed worse on the matching task when the source of interference (odor stimulus) was from the immediately preceding trial compared to when they were from trials further back in the session but only for the 0 s retention interval. These results are compared to previous work examining the effects of proactive interference on working memory in other species.

Keywords: dog, working memory, proactive interference, matching-to-sample

Effects of proactive interference on olfactory memory in dogs

In natural settings, animals are constantly encountering new objects and information. At some point, memory for these stimuli can be taxed to the point of failure (e.g., forgetting). Cognitive psychology has long been interested in understanding these failures of memory (Wixted, 2004), and interference from previously encountered stimuli is one possible explanation (Keppel & Underwood, 1962). Like humans, nonhuman animals, are susceptible to intrusions of stimuli into memory. These intrusions can produce interference that can cause confusion during remembering and can be either proactive (earlier memories cause confusion at a later moment) or retroactive (later memories cause confusion of past moments). Together, these sources of interference can help account for the nature of memory (Wright, 2012).

Proactive interference (PI) is a common explanation for forgetting and its effects are primarily assessed in tasks that use working memory (WM), or the ability to hold and use memories of a stimulus for the length of a session (Dudchenko, 2004). PI is a critical process of interference theory (Keppel & Underwood, 1962). That is, the influence of PI is one way to explain how information can enter the brain, be processed, and stored, but cannot be accurately retrieved (Ceraso, 1967). PI can increase both within a session and across sessions, and is due to the repetition of stimuli, either during a single session (within-session PI) and/or from reusing the same stimulus set each session (across session PI). Both types of PI can be mitigated, or bolstered, by decreasing or increasing the number of repeated stimuli used throughout the experiment, respectively (Wright, 2018).

A favored procedure for comparative studies of PI on memory is the delayed matching-to-sample task (dMTS). In a typical dMTS experiment, each trial consists of a series of phases. First is the sampling phase, where a sample stimulus (e.g., red circle) is presented to the subject

before being removed or made unavailable. Second is the retention phase, where subjects must retain information from the sample item for a certain amount of time (i.e., retention interval) during which the sample stimulus is absent. The retention interval can vary greatly in duration from seconds to hours (e.g., Overman & Doty, 1980). Third is the comparison phase, where a copy of the sample (e.g., red circle) and a non-matching comparison stimulus (e.g., red triangle) are presented at the same time. The correct response is to choose the comparison stimulus (i.e., red circle) that matches the sample presented in the first phase, prior to the retention interval.

A similar task, the same/different (S/D) procedure, requires subjects to compare pairs of stimuli. A key difference between S/D tasks and dMTS is that in S/D, subjects must make a differential response depending on whether the stimuli in the pair are the same or different. For example, Katz, Wright, and Bachevalier (2002) trained monkeys on a S/D task where monkeys were first presented with a sample stimulus (e.g., a photograph of buildings) and then presented with either a copy of the same stimulus, or a different one. For trials in which the two stimuli were the same, the monkeys were rewarded for touching the second (matching) image, and for trials in which they were different, they were rewarded for touching a small rectangle, denoting a "different" response. Importantly, animals in these experiments benefit greatly from an observing response to the sample stimulus (Katz et al, 2007). An observing response can vary between sensory modality and task, but typically requires the subject to physically contact the stimulus (e.g., touch a sample stimulus 10 times). Results from studies using each task have shown that PI can be mitigated, or bolstered, by decreasing or increasing the number of repeated stimuli used (as either sample or incorrect comparison) throughout the experiment (Wright, 2018).

In MTS as well as S/D tasks, PI occurs when the same stimuli switch roles as sample or incorrect comparisons continuously within an experimental session. Thus, repeating stimuli causes an increase in PI (Wright et al., 1986) within a session. One way to manipulate this repetition in MTS is to change the size of the pool from which stimuli are drawn to construct each session, referred to as the set size (Wright, 2007). PI builds up most quickly, and to the highest degree, with a small set size. For example, consider an MTS session with a set size of 2 (e.g., orange circle, blue circle). In this case the stimuli are repeated every trial, sometimes as the sample/correct comparison and sometimes as the incorrect comparison, and within-session PI continues to increase as the session progresses. As set size increases, PI decreases to the point where there can be no within-session interference (e.g., trial-unique). In trial-unique sessions stimuli are not repeated during a session, and hence there is no within-session PI. The effect of set size on memory has been a point of interest for decades (for a review see Wright, 2007).

An additional factor in this procedure is how interference transfers from one trial to the next (Wright et al., 1986), a measure of intertrial PI. On any given pair of consecutive trials, there are several ways for intertrial PI to transition from one trial to another, depending on specific pairings. When the sample is the same from one trial to the next, it is considered a positive transfer trial, where the effects of PI will be mitigated due to the lack of change. Negative transfer trials occur when the previous trial sample changes between trials and is now the incorrect comparison. For such negative transfer trials, performance drops relative to positive transfer trials. Another factor is the outcome of the previous trial. Animals tend to perform worse on rewarded negative transfer trials, whereas rewarded positive transfer trials typically lead to better accuracy (Moise, 1976). That is, if on a negative transfer trial, the previous trial was rewarded, there is often worse accuracy on the trial following the rewarded trial (i.e., the second

trial in a negative transfer pair of trials). The inverse of these is also true, where nonrewarded negative transfer trials tend to lead to higher accuracy than nonrewarded positive transfer trials.

Another way to manipulate repetition is to add interfering probes during trials in which there is otherwise no interference (i.e., trial-unique; no PI) sessions herein referred to as probe trials. Two previous studies used this method for manipulating the locus of PI in pigeons (Wright et al., 2012) and monkeys (Devkar & Wright, 2016). In these studies, interfering probe trials (PI probes) were inserted into trial unique S/D sessions. These probes were trials in which the incorrect comparison stimulus had previously appeared as a correct sample. The presentation of probe trials varied in the number of trials since the comparison stimulus had last appeared in the session. For example, in some probe trials the comparison stimulus might have appeared on the immediately previous trial, or it could be 2, 4, 6, 8 or 16 trials since it first appeared in the session. Additionally, retention intervals occurred between the sample and comparison stimuli. One delay was short (1 s), and the other was a longer delay of 10 seconds for pigeons (Wright et al., 2012) and 10 and 20 s for monkeys (Devkar & Wright 2016). This manipulation allowed the researchers to examine PI both as a function of time (e.g., delay) and number of intervening trials (e.g., probe displacement), as well as an interaction between these effects. Importantly, pigeons (see Figure 2.1) showed worse interference with an increase in time (1 s vs. 10 s), number of intervening trials, as well as an interaction between these two factors, while monkeys (see Figure 2.2) showed an effect of number of intervening trials only. This indicates a potential qualitative difference between pigeon and monkey working memory. For monkeys, interference is only due to the increase of relevant events (i.e., the number of intervening trials) but is not time based. That is, monkeys experienced interference when there was stimulus repetition, regardless of the duration of the retention interval. This explains differences in PI found by Devkar and Wright

(2016) and other studies where monkeys show much stronger PI effects. For example, when composing MTS or dMTS experiments, smaller set sizes will necessarily increase the repetition of relevant events (trials), in turn increasing the overall amount of PI and decreasing accuracy. Indeed, early evidence of dMTS with monkeys suggested they had almost no working memory duration, as their accuracy over delays of just a few seconds was near chance when PI increased to a maximum degree, while reducing PI improved accuracy (Overman & Doty 1980; Wright et al., 2018). Conversely, pigeons show significant effects of intervening trials, delay, and an interaction between these factors. The interaction is the critical component of these experiments, and fully shows an effect of time-based interference. These data cannot be interpreted as loss due to decay because there is no effect of time at baseline trials, where there is no within-session interference and almost no across session interference (see Wright et al., 2012 for modeling of the data).

Expanding the number of species beyond pigeons and rhesus monkeys tested in this procedure can provide information on how time-based and event-based interference have evolved. One species to consider is the dog, for which there is great increasing interest across scientific disciplines in understanding their cognitive processing (Bruce et al., 2021). This is especially important as dogs play a variety of roles in human society, from security and protection, explosives and disease detection, emotional and physical support, companionship, to potential models of human aging (Ruple et al., 2022). Memory and proactive interference can influence performance in each of these roles and has implications for training dogs to perform these roles. Therefore, developing procedures for exploring memory and cognition can lead to improvements in dog welfare and the efficacy of dogs in specialized roles.

Recently, we developed a procedure for training canines to perform olfactory MTS and dMTS to test for abstract-concept learning and working memory (Krichbaum et al., 2021; Lazarowski et al., 2021). Krichbaum et al. (2021) tested the effects of PI at different retention intervals to disassociate the effects of time and PI in dMTS. Dogs experienced dMTS sessions that had been constructed using three different set sizes, each corresponding to the degree of increasing PI (e.g., high, moderate, and no-PI) in a 24-trial session, with varying delays. First, there was the no-PI session which was trial-unique (i.e., each odor appears only once). Second was the moderate-PI condition where six odors were used equally as often, leading to some PI in each session. Last, there was the high-PI condition, where two odors were used in each session, creating a high amount of PI due to constant repetition (i.e., each odor reappears on every trial). Dogs did worse in the high-PI condition than in both moderate and trial-unique sessions. In the high-PI sessions dogs' accuracy was above chance (50% correct) only when there was a 0 s retention interval. The results demonstrated that dogs can be trained to a high level of accuracy on dMTS (greater than 85% correct) yet are still susceptible to the effects of PI.

In the current study, two experiments further tested the effects of PI in dogs. In Experiment 1, set size was manipulated to explore the effects of repetition within a session on dog performance in dMTS only at the 0 s delay instead of using multiple delays within a session (cf. Krichbaum et al., 2021). As in Krichbaum et al., the set size for each session varied in the amount of repetition, and therefore the amount of within-session PI. Each session comprised either 2, 6, or 48 odors. In Krichbaum et al. (2021), there was only an effect of PI at the 2-odor set during 0 s delays. Thus, for this experiment, we expected that performance would be worse in the 2-odor set in relation to the 6-odor and 48-odor sets. We also analyzed the 2-odor set for the effects of intertrial interference (cf., Wright et al., 1986). Negative transfer trials where the

previous trial was rewarded were expected to have worse overall accuracy than other combinations, especially positive transfer trials where the previous trial was rewarded. Alternatively, dogs may have a tendency to perseverate on their previous choice, meaning that regardless of reward, dogs will suffer from intertrial interference effects when the previous choice and current sample differ. On trials where the current sample is the same as the dog's previous choice, there will be higher accuracy and no deleterious effect of intertrial PI. In this view, interference would occur because memories of the current trial choice conflict with memories of the previous trial choice. When the stimuli were the same, there was no deleterious effects of PI, but when the stimuli were different, there was a deleterious effect of PI. Worse accuracy in the dMTS task would indicate conflicting memories of the current sample and previous samples. In Experiment 2, to characterize dogs' representation of PI as either time or event-based, we adapted the PI probe experiments of Wright et al. (2012) for olfactory dMTS. The effects of delay (0 s vs. 20 s) and number of intervening trials (n-1, n-6, n-12, and no-PI) were tested. If PI in dogs is functionally due to the effects of time, then the effects of delay, the number of intervening trials, and the interaction between these two, would be significant. This result would suggest that dogs are more like pigeons in their representation (i.e., the reference memories of the sample used at test) of PI. Otherwise, if neither delay nor the interaction are significant, this would suggest that dogs are more like monkeys and that event-based PI might be shared among mammals broadly.

General Procedures

Methods

Subjects

Six Labrador retrievers (4 female) served as subjects for this experiment. Ages ranged from two to six years, (mean age: 4.17 years). Dogs had previous training history in scent detection. After initial training, tests of MTS abstract-concept learning (Lazarowski et al., 2021) and subsequent dMTS training with set sizes of 2, 6, and 48 odors with delays of 0, 30, 60, and 90 s (Krichbaum et al., 2021) was administered. The data for Experiment 1 were collected alongside the data reported by Krichbaum et al. (2021). After the abstract-concept learning testing (Lazarowski et al., 2021), dogs began dMTS training with variable delays using the trial-unique 48-odor set. After this initial dMTS training, the dogs were tested on each of the smaller set sizes, starting with the 0-s delay sessions reported here. Thus, each dog completed the 0-s delay 2-odor and 6-odor sessions before the corresponding session of 2- and 6- odor dMTS session as in Krichbaum et al. (2021). The data from Experiment 2 were all collected immediately following the last dMTS session. Dogs were housed in kennels with indoor/outdoor runs at Auburn University's College of Veterinary Medicine. Auburn University's Institutional Animal and Care Use Committee approved the animal use. Approval was granted by the Auburn University Institutional Animal Care and Use Committee (protocol: #2018-3334). Dogs were tested in the following sequence: initial MTS training, abstract-concept learning as described by Lazarowski et al (2021), Experiment 1 of this study and experiments reported by Krichbaum et al. (2021) and ending with Experiment 2 of this study. Dogs were tested on one condition at a time, and only one session per day. Typically, two dogs were tested each day.

Stimuli and Apparatus

Stimuli were 48 household spices (e.g., ground cinnamon; from The Great American Spice Company, Rockford, MI, USA) and essential oils (e.g., almond extract; Anjou Naturals, Fremont, CA) used primarily for cooking (see Table 1 for list of odors). To present odors, cotton

pads (Swisspers® 100% cotton rounds pads) were first saturated with the odor by storing them in glass mason jars with approximately 28 g of powder or 3-4 drops of each essential oil. Cotton pads were placed into a perforated tin at the beginning of each session. These perforated tins were kept in a container unique to each odor.

Testing took place in an enclosed arena (6.5 x 6 m; Figure 2.3) in a temperature-controlled building at Auburn's Canine Performance Sciences. In the arena, there were six cinderblocks (19 x 19 x 19 cm) placed on wooden platforms (28 x 28 x 18 cm) that served as possible locations for odors. Within each cinderblock were paint canisters that could hold an odor tin. Each location, regardless of the presence of an odor tin, looked the same from the entrance of the arena. Cinderblocks were arranged in a semi-circle formation, approximately .5 m apart from each other, and 2.7 m from the entrance to the arena. Thus, dogs had to search each location to find odors. A sample odor, which provided the dogs with the correct choice in the arena, was presented to the dogs before they could enter the test arena. The sample odor could be in one of the three cinderblock/paint canister locations outside the arena. Each session was recorded by HD camera (GoPro Hero 5), which also was used as closed-circuit television (i.e., CCTV) to observe and live-score each session.

Task: Olfactory dMTS

There were 24 trials in each session. A trial began when experimenter 1 signaled to the handler that the trial was ready. At the beginning of each trial, dogs were directed to search the sample location, which varied randomly across three possible locations. When they made an observing response, defined as fully putting their snout in a paint canister and freezing for 1 s (often referred to as a "change of behavior," Minhinnick et al., 2016), the handler marked the response with a clicker and the dog entered the arena to search the array off-leash with all

experimenters and handlers out of view. A dog could search in any direction, and typically searched from right to left (all odors were balanced so that either search direction led to the correct choice first an equal number of times). A dog indicated a choice by sitting next to the cinderblock with the odor in it. Handlers, who were kept blind to the location of each odor, signaled when a response had been made, and experimenter 2 relayed whether the dog was correct or incorrect. For correct responses, handlers again clicked, at which point the dog ran back to the handler for play with a chuck-it® ball. For incorrect responses, handlers recalled the dog and did not reward them with the ball or engagement. The handler held the dog until the next trial was ready. During delay trials, the sample canister was removed from the sample area and the dog was held at the entrance to the arena before sending the dog into the arena in order to remove access to the odor during the delay. There was an intertrial interval (ITI) of about 30 seconds, varying only slightly depending on individual dogs, handlers, and experimenters. Between sessions, the experimenters swept and cleaned the arena. Odors were always handled with gloves, and odorized cotton pads were replaced prior to the first session of the day.

Experiment I: Set Size Testing

Dogs began set size testing after testing on three sessions of 48-odors (trial unique). Dogs were then tested with two different odor set sizes: 2-odors and 6-odors. Each set size was tested twice, counterbalanced for order across subjects. A different set of odors were used each session to avoid across-session PI. In the 2-odor set, carob and amaretto were used in one session, and coriander and apple in the other session. For the 6-odor set, allspice, apricot, cotton candy, pecan, parsley, and chamomile were used in one session, and butterscotch, cinnamon, garlic, mustard, root beer, and thyme were used in the other session. 6-odor sessions were balanced such that each odor appeared both as the sample and incorrect distractor 4 times each. The same odors

were used for each dog to rule out potential differences between dogs due to odor, which may have been more likely with only six dogs as subjects.

The 2-odor sessions were arranged to test for four intertrial progressions (Wright et al., 1986). Specifically, the four types of intertrial progression are: odor A repeats as sample, odor A switches from sample to incorrect comparison, odor B repeats as sample, and odor B switches from sample to incorrect comparison. These four intertrial progressions have been called positive (PT) and negative transfer (NT). When the sample repeats, there is a positive transfer between trials (i.e., the previous trial memories will not cause a disruptive intrusion). When the sample changes there is a negative transfer (i.e., previous trial memories will be disruptive). Each transfer type occurred 12 times in each session, allowing us to analyze the intertrial PI effects.

Data Analysis

Data were analyzed in R (version 4.0.3) using a generalized linear mixed-effects model (GLMM), binomial family distribution, with individual dog ID as a random factor (lme4 package; Bates et al. 2015). To fit a binomial distribution, accuracy was coded as 1 for correct and 0 for incorrect (as opposed to using a percent correct score as in linear regression). Accuracy was determined as a function of set size (2, 6, 48), coded categorically as small, medium, and trial-unique. Trial (1 to 24) was also included as a variable. The initial formula for the logistic regression was as follows: Accuracy ~ set size + trial + trial * set size + (1|Dog), where the term (1|Dog) specifies random effects of individual dog.

A second analysis explored the effects of positive and negative transfer in the 2-odor condition. Each trial is coded as either positive transfer (PT) or negative transfer (NT). Reward is also included as a factor and coded as whether or not (yes or no) the previous trial was rewarded.

The formula for this logistic regression was as follows: Accuracy ~ trial type + reward + reward * trial type, (1|Dog).

Results and Discussion

Figure 2.4 shows the effect of set size on mean accuracy. PI had an effect in the 2- and 6-odor conditions relative to the 48-odor condition. There was a significant main effect of set size, such that dogs had lower accuracy on the 2-odor set (M = 74.53, SE = 4.40) than the 48-odor set (M = 87.15, SE = 1.08; z = -3.34, p < .001) as well as with the 6-odor (M = 76.01, SE = 3.77) set relative to the 48 odor set (z = -3.60, p <.001). There was no significant difference between the 2-odor and 6-odor set sizes (M = 76.01, SE = 3.77; z = -0.31, p = .756). Five of six dogs showed an effect of interference (i.e., lower percent correct) in the 2- or 6-odor sessions. The main effect of trial and the interaction between set size and trial (z = -1.19, p = .235) were not significiant, therefore, the final model was accuracy ~ set size + trial + (1|Dog).

Figure 2.5 illustrates the combined effects of intertrial PI and the impact of reward (i.e., that the previous trial had been rewarded) on mean accuracy (i.e., percent correct) for the 2-odor set size. There were significant effects of reward (reward: M = 74.77, SE = 5.19; non-reward: M = 73.43, SE = 6.13; z = -2.89, p = .004) and trial type (PT: M = 76.92, SE = 6.06; NT: M =71.94, SE = 4.10; z = -2.6, p = .009) and the trial type x reward interaction was also significant (z = 3.45, p < .001). Therefore, two separate GLMMs examining the effect of transfer type (PT or NT) were analyzed for previous rewarded or non-rewarded trials seperately. When the previous trial was rewarded, accuracy on PT (M = 81.31, SE = 5.22) was higher than NT (M = 68.47, SE = 1.47) trials (z = 2.37, p = .018), while when the previous trial was not rewarded, dogs performed better on NT (M = 85.71, SE = 2.93) than PT (M = 63.89, SE = 6.71) trials (z = -2.47, p = .013).

In Experiment 1, the effects of within-session and intertrial PI on accuracy in dogs were shown. Repetition from the 2- and 6-odor sets caused increased PI and worse overall accuracy compared to trial-unique sessions in this task. These results are in line with the data from 0 s delay condition of Krichbaum et al. (2021), where dogs perform worse with a 2-odor set (72.22%) than 6 (85.56%) and 48 (87.78%) odor sets. However, we found a significant difference in accuracy between 6 and 48 odor sets, indicating that by removing variable delays from each session, the effects of PI were more robust for 6 odors at the 0 s delay. Perhaps in the previous study the more difficult, longer delays created a contrast effect which allowed the dogs to combat PI at the 0 s delay. In addition, the longer delays (30, 60, 90 s) created greater time differences over trials, which may have helped to combat PI in the previous experiment and diminished PI in the 6-odor condition. The lack of a trial effect indicates that the observed effects of PI occurred early in a session and did not increase throughout a session. Perhaps sessions longer than 24 trials would show an increasing effect of PI build up due to increasing stimulus repetition. The lack of effect of trial and the interaction suggests that the effects of PI occurred toward the start of session, and did not increase further over trials.

In the trial type analysis (Figure 2.5), there was a significant interaction between reward and trial type where dogs tended to perseverate on behaviors that were recently rewarded, causing severe interference on negative transfer trials when they were previously rewarded, but not when the previous trial was unrewarded (17.24% difference). On positive transfer trials, dogs performed best when the previous trial was rewarded, and worse when the previous trial was not rewarded (17.42% difference). Dogs did better on both rewarded positive transfer trials and nonrewarded negative transfer trials, and worse on rewarded negative transfer trials and nonrewarded positive transfer trials. These results replicated similar findings in pigeons

(Roberts, 1980) and pig tailed macaque monkeys (Moise, 1976). Table 2.2 (adapted from Wright et al., 1986) shows the effects of PI as a function of transfer and either reward or previous choice in our study, as well as Roberts (1980) and Moise (1976). On the left column is transfer type, either positive transfer (PT) or negative transfer (NT) as described previously. The next column describes the outcome of the previous trial (N-1) in terms of reward or nonreward. Under % correct on trial N is the accuracy for each species as a function of trial transfer type and reward. The last column reinterprets the accuracy under % correct on Trial N as a function of trial type and the animals' choice on N-1, where "same" means the current sample is the same as the previous trial choice, and "different" means the current sample is not the same as the previous trial choice. When the previous choice and the current sample are the same, dogs show no effects of PI. However, when the previous choice and the current sample are different, dogs show a significant effect of PI. Monkeys and pigeons show similar effects. What these data show is that intertrial interference is less influenced by reward outcomes than by what stimulus the animal just selected during the choice phase on the previous trial (cf., Roberts 1980; Wright et al., 1986). Of note, while these findings show a qualitative similarity across species, there is a quantitative difference. The effect is on the order of 5-8% in pigeons and monkeys but a 17% difference in dogs. That is dogs seem to be more influenced by what stimulus was selected on the previous trial than the consequences of that choice. It is important to note that the sources of intertrial interference are not all or none. For example, if dogs were only controlled by their previous choice, then the difference between the positive transfer rewarded vs. non-rewarded trials would be 50%.

Influence from the previous choice has also been shown in a variation of the dMTS, the delayed matching-to-position (DMTP; Dunnett & Martel, 1990). Rats were trained to press a

lever that was inserted into one of two locations in an operant chamber. Pressing the lever started the delay period, where the lever was removed for the duration of a retention interval (such intervals ranged from 0 to 24 s in this study). After the period, levers were inserted into both locations, and rats had to press the lever at the same location as before in order to obtain a reward. Pressing the nonmatching lever led to a time out period. Rats were susceptible to the effects of interference from the proceeding trial only, especially at longer retention intervals. Directly comparing the effects of previous sample vs. previous choice found that choice produced stronger intertrial interference effects. This study (Dunnett & Martel, 1990) also found that longer intertrial intervals reduced the interference effects. Roberts (1980) and Moise (1976) used intertrial intervals of 1 s or 20 s, and 15 s, respectively. The current study on average had a 30-s intertrial interval. It would be worth exploring the effects of different intertrial intervals on interference in dogs in follow up experiments. An important takeaway from these experiments is that this effect is not bound to olfactory stimuli as in our experiment, but also found in spatial (Dunnett & Martel, 1990) and visual (Moise, 1976; Roberts, 1980) matching tasks. This suggests that the effect of previous choice is a true effect of PI (Wright et al., 1986), one that reflects common memory processes in each sensory modality.

Experiment II: Proactive interference Probe

Experiment 1 found that proactive interference is not only influenced by the memory of repeated stimuli (2 and 6-odor sets had worse accuracy than the trial unique set) but also the memory of the previously chosen stimulus. In Experiment 2, we addressed whether such memories are event or time-based.

Procedure

Each session was 24 trials long and had three of each interference trial separation (n-1, n-6, n-12) embedded within a session (Table 2.3 is a representation of a session). For example, in Table 2.3, trial 6 has an n-1 trial separation because the incorrect choice (maple) was the sample on trial 5 (n-1), trial 8 has an n-6 trial separation because the incorrect choice (parsley) was the sample on trial 2 (n-6), trial 15 has an n-12 trial separation because the incorrect choice (oregano) was the sample on trial 3 (n-12). The remaining 15 trials are all trial-unique for that session (referred to as No-PI).

Sessions were conducted with a 0-s delay or a 20-s delay condition. In the 0-s delay condition, dogs would immediately enter the arena after they made an observing response to the sample, indicating they had smelled the sample odor. In the 20-s delay condition, handlers held the dog just outside and out of view of the arena for 20 s before sending the dogs into the arena. There was one session conducted for each condition, which was counterbalanced between dogs. All other procedural details were the same as in Experiment 1.

Data analyses

Data were analyzed in R (version 4.0.3) using a generalized linear mixed-effects model (GLMM), binomial family distribution, with individual dog ID as a random factor (lme4 package; Bates et al., 2015). To fit a binomial distribution, accuracy was again coded as 1 for correct and 0 for incorrect (as opposed to using a percent correct score as in linear regression), just like in the previous analysis. Accuracy was determined as a function of trial separation (i.e., number of trials since the interfering stimulus last appeared: 1, 6, 12, No-PI), delay (0 s, 20 s), and a trial separation x delay interaction. The logistic regression had the following formula: Accuracy ~ trial separation + delay + trial separation * delay, (1|dog), where the (1|dog) specifies random effects.

Results and discussion

Dogs showed an effect of trial separation that interacted with delay such that as the trials are further separated in the sequence (i.e., there is greater trial separation) accuracy improves with the 0-s delay but not the 20-s delay, as shown in Figure 2.6. The analyses revealed the significant main effect of trial separation, (n-1: M = 77.78%; n-6: M = 69.44%; n-12 : M = 91.67%; no-PI: M = 85.56%; z = 2.62, p = .009).The main effect of delay was not significant (z = -0.70, p = .486), and the interaction between the trial separation * delay was significant (z = -1.97, p = .049). Two separate GLMMs found that the interaction was driven by the significant effect of trial separation in the 0 s delay condition (z = 2.79. p = .005), and non-significant effect of trial separation in the 20 s delay condition (z = 0.09, p = .925).

In Experiment 2, we sought to better characterize the proactive interference of odors in dogs. To do this, we adapted procedures from Wright et al. (2012) and Devkar and Wright (2016). Wright et al. (2012) found evidence in pigeons of a type of PI characterized by intrusive memory cues due to time, whereas Devkar and Wright (2016) found that monkeys suffer from intrusive proactive memories based on the number of similar events. Only when interfering events occurred in immediate succession did monkeys suffer significant decreases in accuracy. The key difference between monkeys and pigeons in the locus of PI is the influence of time. Interference in monkeys is functionally related to the number of events between the probe and the first time the stimulus is experienced regardless of the amount of time between each event (Wright, 2018). Pigeons, by contrast, showed strong effects of time. When pigeons are comparing the stimuli during the test phase of the S/D task, they are comparing it to memories of the sample. Exactly which memories of the sample depend on the elapsed time since the sample was viewed. Whereas when monkeys remember the sample, interference comes from other

recent events (i.e., the previous trial). Our results are tentative but suggest that dogs might be using event-based memory in the task. To elaborate, they did not show a significant effect of delay; however, the interaction between delay and trial separation was significant. Further analysis indicated the interaction was due to only an effect of interference during the 0 s condition, and there was no effect of trial separation in the 20 s session. Perhaps the 20 s delay periods created an effect where dogs were no longer confusing the previous trial samples as they could better represent each sample as a separate event. While not exactly replicating the results from Devkar and Wright (2016), the fact that the effect was limited to the 0-s delay condition suggests that dogs were more similar to monkeys suggesting event-based memory in dMTS. If memory were time-based, the effect of PI over trial separation would have been stronger in the 20-s than the 0-s delay condition.

However, there are some caveats to these conclusions. First, procedurally the experiments are different. The pigeons and monkeys in the previous studies were trained on a same/different (S/D) discrimination which, while similar to MTS, might require different memory systems (Shettleworth, 2010, p. 201-202). Second, pigeons and monkeys were tested for more sessions than in the present study, therefore diminishing power in the present study. While the results were statistically significant, they were variable, and the result could change with a larger sample size or more sessions. In summary, we view these results as tentatively suggesting that dogs may have an event-based experience of PI yet replicating these results in the future is important.

General Discussion

These experiments show the effects of proactive interference on dogs' working memory in an olfactory dMTS task. In Experiment 1, we found that dogs were susceptible to proactive interference. Interference reduced accuracy in both the 2-odor and 6-odor conditions relative to

the 48 trial-unique condition. We also found an interaction between reward and susceptibility to interference for PT and NT trials. When reward contingency was consistent with transfer (i.e., rewarded positive transfer trials and nonrewarded negative transfer trials) dogs showed very high accuracy relative to inconsistent trials (i.e., nonrewarded positive transfer and rewarded negative transfer trials). This interaction indicates dogs were influenced more by the choice they made on the previous trial than the response outcome. In Experiment 2, we found that dogs were sensitive to PI probes only at the 0 s delay. There was also no overall effect of delay (0 s vs. 20 s), all together suggesting, tentatively, that dogs may have an event-based memory for odors.

While there is past research on variations of the dMTS using dogs (Chan et al., 2002; Fiset et al., 2003; Kucœmierek & Kowalska, 2002), none of these studies other than Krichbaum et al. (2021) have specifically sought to examine the effects of set size on working memory. One study used trial unique stimuli with dogs in an auditory variant of the dMTS and found that there was no within-session PI (Kucœmierek & Kowalska, 2002). Other studies have used a visual delay non-matching-to-position task (vDNMP; Chan et al., 2002), where dogs were presented with a tray that had an object on either the left or right side of it. Dogs were rewarded for displacing the object, after which the tray was removed for a retention interval. After this interval, the tray was brought back, this time with objects on both sides; the dog was rewarded for displacing the item on the opposite side from the first object. The limited number of locations would seem to generate a large amount of PI; however, younger dogs were still accurate up to delays of 110 s, while older dogs struggled with delays of 30 s.

Other animals have been evaluated for the effects of PI (for a review see Wright, 2006). For example, Overman and Doty (1980) found that monkeys' memory during dMTS is greatly affected by set size. At a short 5 s delay, monkey accuracy drops to 70% for 2 stimuli sets,

compared to over 90% for both 100 stimuli and novel stimuli sets. Pigeons similarly show these effects of PI when delay is zero or just a few seconds (Zentall & Hogan, 1974). As mentioned previously, Dunnett and Martel (1990) found effects of PI in a spatial DMTP task in rats. One point of interest is that both of the spatial delay tasks seemed to be set up for a large degree of interference through the small set sizes in each experiment. However, dogs and rats did not seem to have much of an effect of PI on accuracy. This could reflect a difference in the way spatial PI is experienced. Perhaps spatial information is represented differently from visual, auditory, and olfactory information, thus dampening the effects of PI.

Future Directions

There are several relevant follow-up studies for both experiments. In the future, ITI is an important variable to manipulate. In Experiment 2, the dogs had an effect of interference for the 0 s delay, and on average an ITI of 30 s. Modulating ITI in an olfactory MTS task, both with dogs and with other species, would be an important next step in understanding this relationship. Devkar and Wright (2016) examined the effects of ITI in their PI study, using either 5 s or 15 s ITI durations. There was no effect of ITI, and the effects of interference were still strongest when the trial number of the interfering stimulus was n-1. While Devkar and Wright did not find an effect of shorter ITI durations, it is unknown how longer durations, such as 120 s, would affect interference. If there was an absence of an ITI effect with dogs this would provide additional evidence of event-based memory. Finding ways to replicate our dog studies with different sensory modalities could be another future direction. We used olfactory stimuli as opposed to visual stimuli in order to take advantage of olfaction, as it is dogs' primary sensory modality. The effects of PI may vary with different sensory systems within a species (e.g., Wright, 1998). Additionally, expanding the species tested on these procedures, especially the PI probe

experiment, would be of interest as this manipulation has only been tested in pigeons, rhesus monkeys, and now dogs. Human participants in particular would provide a valuable comparison point, and so would rats, as common laboratory animals. Previous studies with rats have shown similar effects of set size, such that rats using only 2 odors during MTS and nonmatching to sample (NMTS) failed to learn and generalize to new odors, but with larger sets the rats succeeded (Lazarowski et al., 2019; Peña et al., 2006). While these studies did not specifically seek to test the effects of set size and PI on rat (N)MTS performance, it is likely that PI played a role, similar to how it affected the dogs in the present studies. An additional reason to expand the PI probe experiment is that olfaction is likely rats' primary sensory modality as well, providing a useful comparison to dogs. The use of a species' preferred sensory modality has been shown to improve overall performance in dMTS tasks (Lind et al., 2015). The use of a favored sensory modality is likely shared between all three PI-probe experiments (vision for monkeys and pigeons, odors for dogs). Testing these and other species on different sensory modalities could reveal functional relationships between modality and interference. The aforementioned future experiments will help to better understand familiarity and episodic memory as it has been argued that the difference between event-based and time-based memory are similar to the differences between episodic memory and familiarity, respectively (Devkar & Wright, 2016; Wright, Kelly, & Katz, 2018).

One consideration of both experiments is the breed used and that these dogs are purpose-bred detection dogs bred for certain characteristics. These traits and their rearing/training history may improve their cognitive abilities. Hence, there may be differences in motivation and trainability between working dogs and companion dogs (Lazarowski et al., 2018). Therefore, translating these findings to companion dogs and other breeds would be premature. Replicating

these experiments with companion dogs of different breeds can elucidate this point of translation. Including other domesticated animals, such as cats and livestock, would be of interest as well. Such an expansion will allow for improved understanding of the evolution of the functional relationships of interference processes and memory.

Conclusion

Dogs play an important role in society as companion, working, service, and model animals. It is important to understand the cognitive aspects of dog behavior as this can have implications for welfare and service. Training working dogs is an expensive and time-consuming practice and understanding cognitive processes of dogs can streamline training as well as reduce frustration from unrealistic expectations placed on dogs in training programs. Improving the process of training dogs improves both the services they provide as well as dog welfare (Cobb et al., 2015). Effective selection is one method for reducing financial cost and improving welfare of training dogs for service (Bray et al., 2021) and requires careful observation of various characteristics. Sensitivity to PI, and willingness to continue working in confusing or frustrating conditions, could be relevant factors, especially as combatting PI may be related to working memory span, (Conway et al., 2003; Jonides & Nee, 2006), which in turn is related to general fluid intelligence (Broadway & Engle, 2010). Understanding these complex cognitive processes in dogs may improve selection and training of detection dogs (Maclean and Hare, 2018).

Dogs are potential models of aging and dementia, both of which are associated with declines in olfaction and increased susceptibility to proactive interference. Dogs are phenotypically diverse and share many of their habitats with humans (Ruple et al., 2022). Dogs, like humans, show white matter demyelination as a sign of aging (Chambers, Uchida, & Nakayama, 2012; Gunning-Dixon et al., 2009; Guttmann et al., 1998). In humans, white matter

degradation has been linked to increased susceptibility to PI (Andersson et al., 2022). Additionally, declines in olfactory functioning are an early sign of forms of cognitive decline, including mild cognitive impairment (MCI) and Alzheimer's disease (AD) (Jung, Shin, & Lee, 2019; Windon et al., 2020). Dogs may be of use in modeling these olfactory related declines and examining whether these age-related PI effects are also found in dogs performing olfactory tasks could provide important behavioral correlates of MCI and AD in dogs and humans.

In this study, dogs showed susceptibility to within-session and intertrial PI solely through the manipulation of the repetition of events, regardless of factors of time. This clearly indicates a role of PI in the forgetting processes of dogs. Previous studies have not explicitly shown intertrial PI effects, or the effects of interference completely separate from any within session effects of delay. This is important for improving the success of working dogs, but replicating these results in applied settings would be useful to see how well these findings translate. In a live detection scenario, for example at a sporting event, there are far more distractions and therefore possible intrusions into the dog's memory, potentially affecting the observed effects of PI. Scent lineup dogs would be an important application as well, as many countries (Ferry et al., 2019) use dogs to link suspects to possible crimes. PI as outlined in the present paper could have disastrous consequences in such situations. Overall, these two experiments represent a further step in understanding dog cognition and memory and has relevant applications to real world situations.

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Table 2.1

List of all odors used in the experiments.

Allspice	Butter	Cloves	Garlic	Peach	Savory
Almond	Butterscotch	Coffee	Lemon	Peanut butter	Strawberry
Amaretto	Caramel	Coriander	Lime	Pecan	Sumac
Anise	Carob	Cotton candy	Maple	Pina colada	Tangerine
Apple	Chamomile	Eggnog	Marshmallow	Pineapple	Thyme
Apricot	Champagne	English toffee	Mustard	Raspberry	Tobacco
Blackberry	Cherry	Fennel	Oregano	Root beer	Turmeric
Blueberry	Cinnamon	Fenugreek	Parsley	Rosemary	Watermelon

Table 2.2

Relationship between accuracy as a function of the prior trial's (N-1) sample, outcome, and choice.

Trial (N-1)		% Correct on Trial N			Trial (N-1)
Sample	**Outcome**	**Dogs**	**Pigeons[1]**	**Monkeys[2]**	**Choice**
Same (PT)	R	81.3%	73.6%	75.3%	Same
Same (PT)	NR	63.9%	68.8%	64.5%	Diff
Diff (NT)	R	68.5%	65.1%	62.3%	Diff
Diff (NT)	NR	85.7%	73.4%	71.4%	Same

Note. PT = Positive Transfer, NT = Negative Transfer, R = Reward, NR = Nonreward, [1]Roberts (1980), [2]Moise (1976). After Wright et al. 1986.

Table 2.3

A representation of trial-by-trial progression of each session. No-PI indicates no proactive interference.

Trial	Sample	Incorrect Comparison	Trial Separation
1	Savory	Lemon	No-PI
2	Parsley	Cotton Candy	No-PI
3	Oregano	Cinnamon	No-PI
4	Apple	Peanut Butter	No-PI
5	Maple	Strawberry	No-PI
6	Tangerine	Maple	N-1
7	Lime	Blackberry	No-PI
8	English Toffee	Parsley	N-6
9	Raspberry	Anise	No-PI
10	Pecan	Fenugreek	No-PI
11	Clove	Caramel	No-PI
12	Marshmallow	Thyme	No-PI
13	Almond	Lime	N-6
14	Turmeric	Rosemary	No-PI
15	Peach	Oregano	N-12
16	Garlic	Apple	N-12
17	Coffee	Clove	N-6
18	Eggnog	Champagne	No-PI
19	Sumac	Watermelon	No-PI
20	Mustard	Sumac	N-1
21	Tobacco	Raspberry	N-12
22	Chamomile	Pina Colada	No-PI
23	Cherry	Apricot	No-PI
24	Butter	Cherry	N-1

Figure 2.1

Mean percent correct for pigeons at each trial number of interfering stimulus (1,2,4,8,16) from Wright, Katz, and Ma (2012). Pigeons show main effects of delay, trial number of interfering stimulus, and an interaction between these factors.

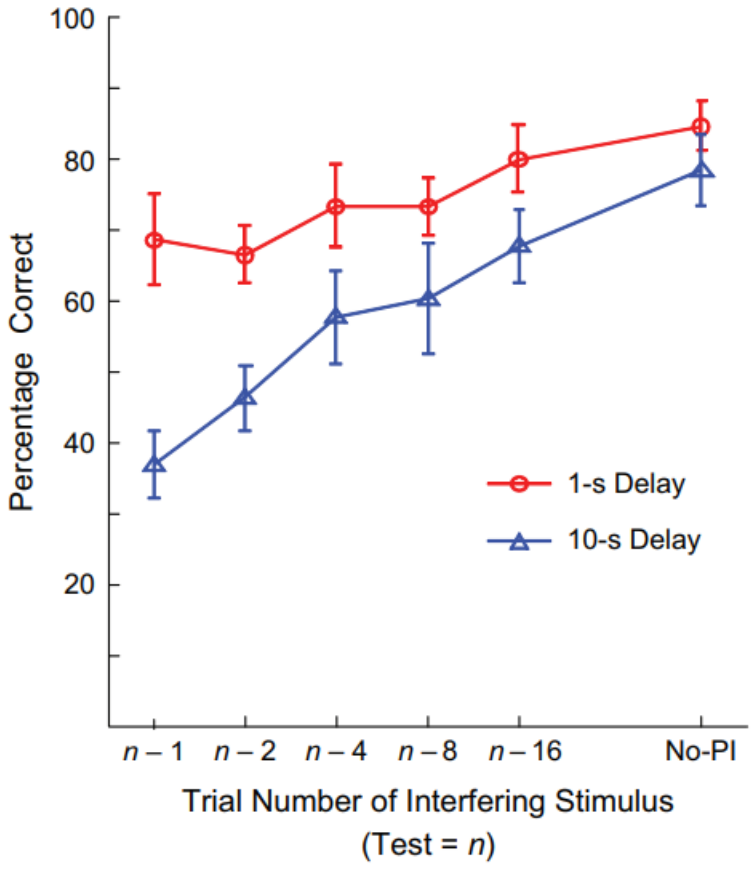


Figure 2.2

Mean monkey performance by delay and trial number of interfering stimulus, from Devkar and Wright (2016). Note that the lines overlap, indicating no effect of delay. Monkeys are only impacted by proactive interference when the repeating events occur immediately after one another.

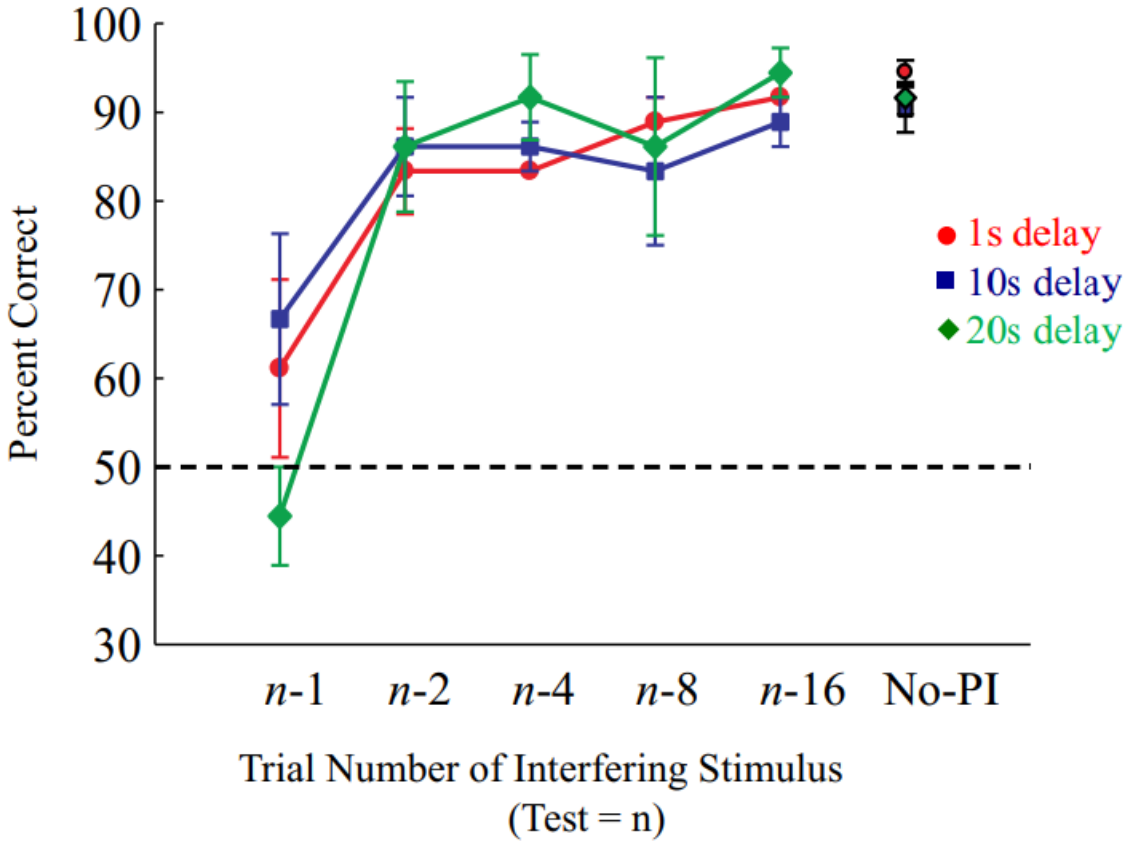


Figure 2.3

Schematic representation of the testing arena. Previously published in Krichbaum et al. (2021). The dotted line represents the path each dog takes on each trial. Prior to each trial, Experimenter 1 places each odor in the predetermined location and then returns to the location marked by E1. At the beginning of each trial, the handler (H), directs the dog from its starting location at the star along the path indicated by the dotted arrowhead lines. Along this path the dog is commanded to search the three potential sample odor locations. At the end of the line, the dog is released into the enclosure to search the six potential locations in whatever order it chooses. Handler 1 remained out of the enclosure, out of view of the dog, and observed the dog via a monitor that displayed a live feed of enclosure and signaled when the dog made a choice. Experimenter 2 stayed in location E2, separated by a low wall. Experimenter 2 confirmed whether choices were correct or incorrect and scored each trial.

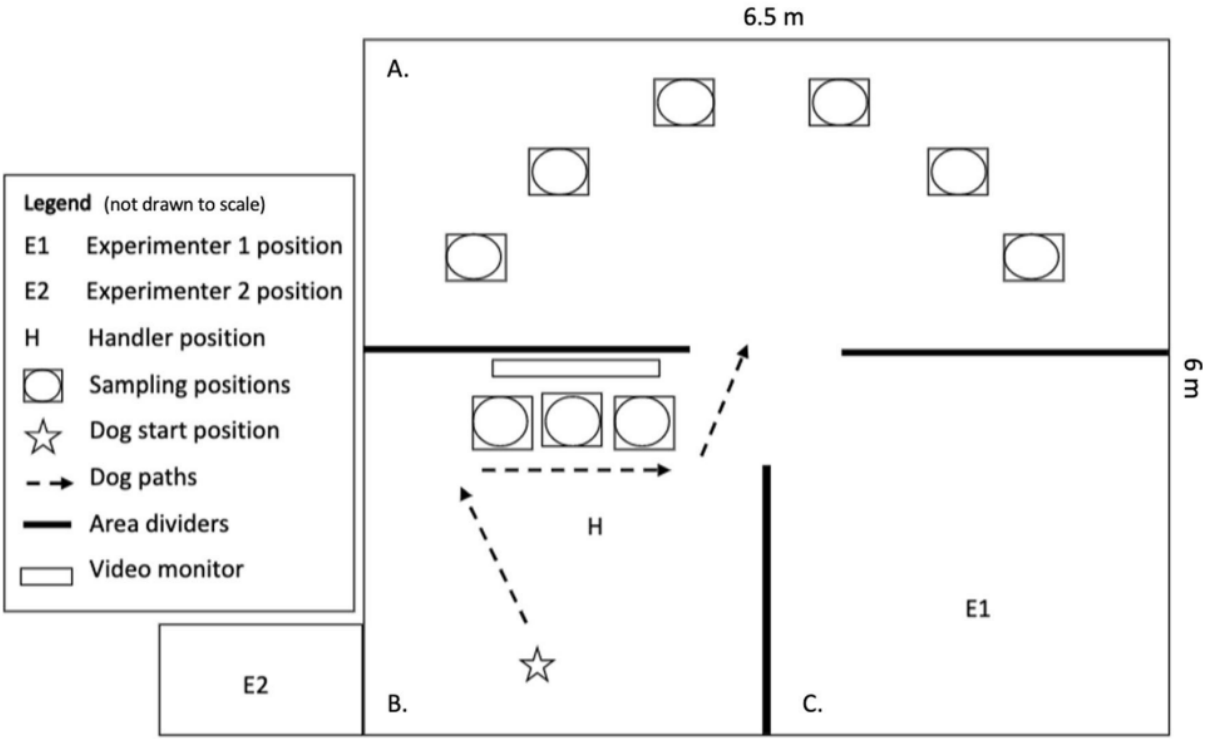


Figure 2.4

Mean and standard error of each set size. No-PI condition (48 odors) had higher overall accuracy than both the 6 and 2-odor sets.

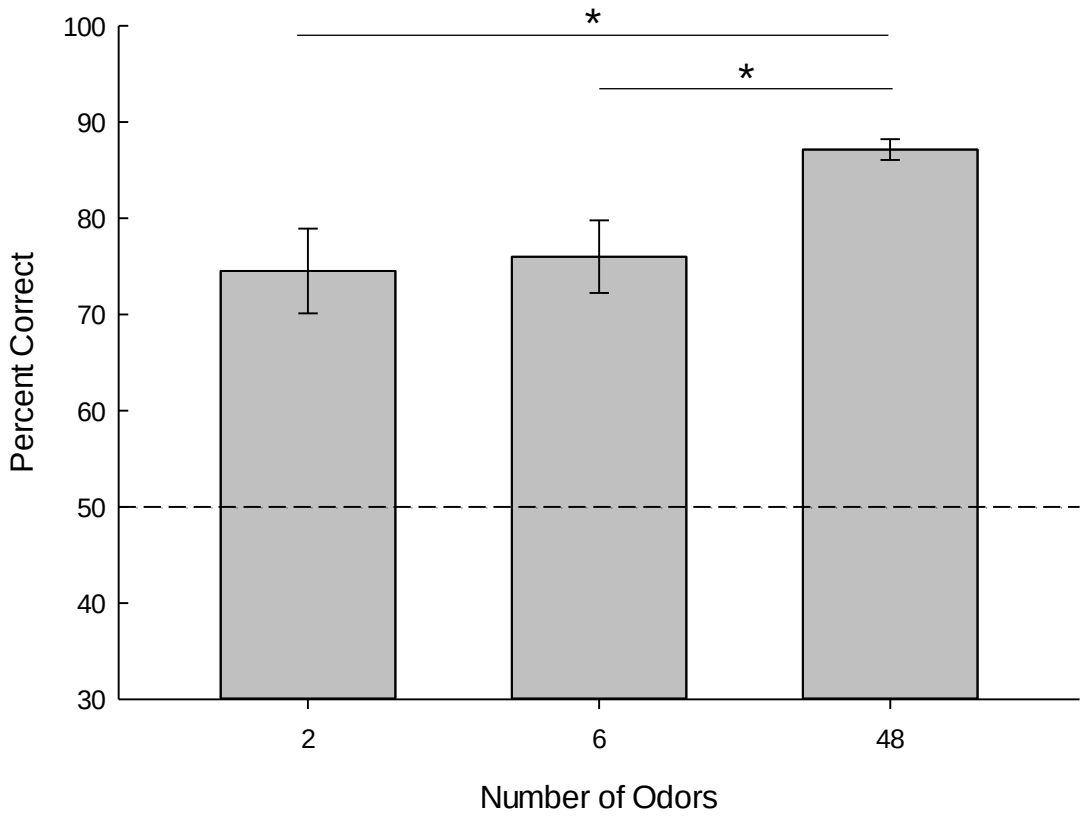


Figure 2.5

Means of each trial transfer type (positive and negative) when the previous trial was rewarded and when it was not rewarded).

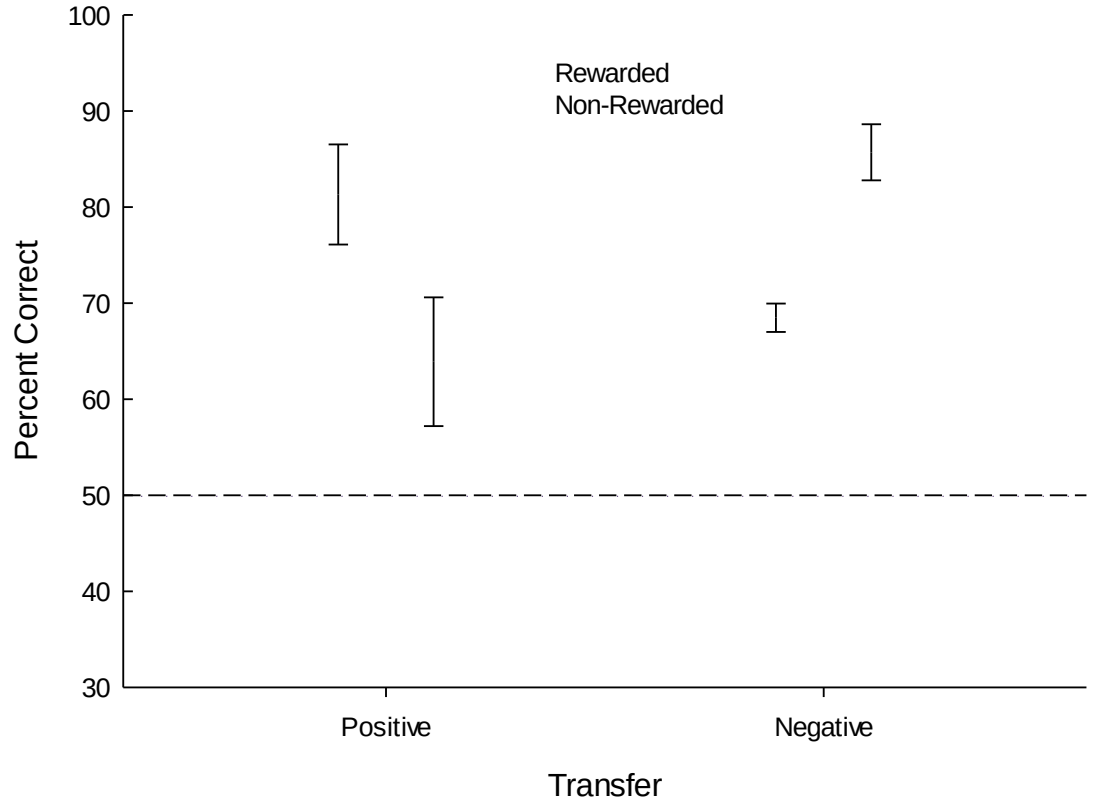
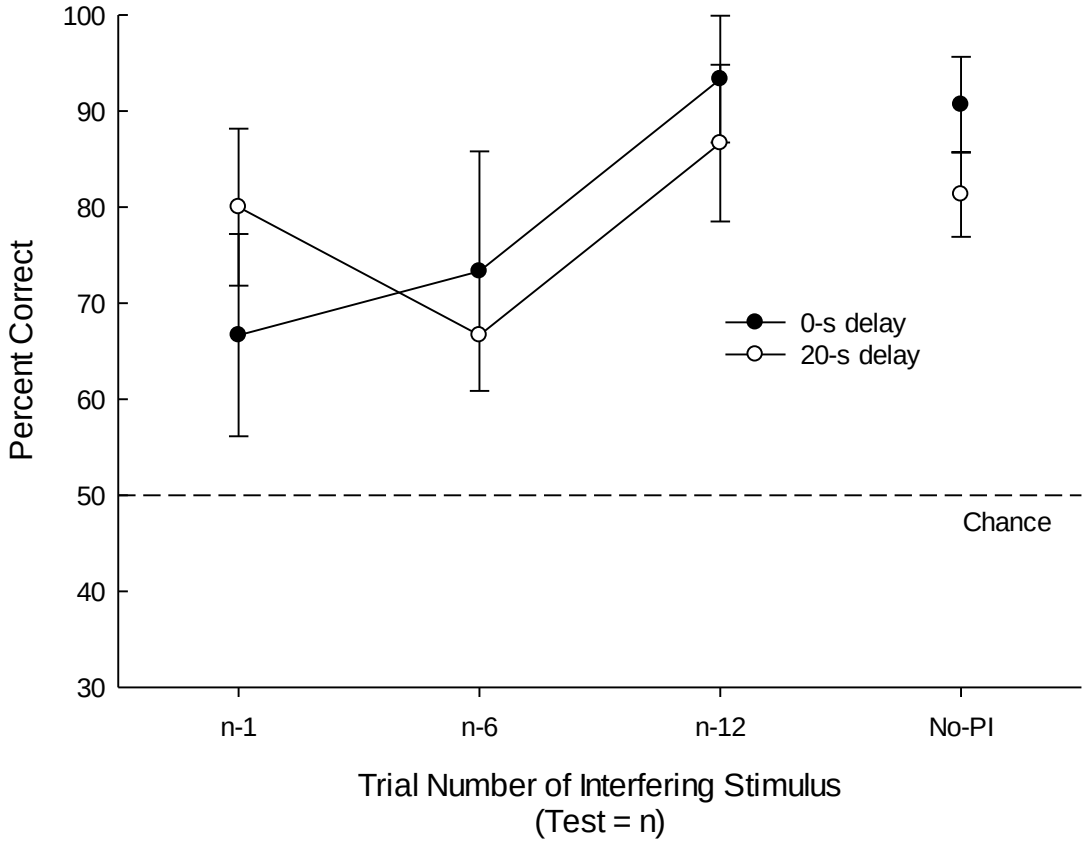


Figure 2.6

Accuracy by delay and interference test. Filled symbols represent mean accuracy across the number of interfering stimulus at 0-s delay, while open symbols represent mean accuracy across the number of interfering stimulus at 20-s delay. Error bars represent standard error. Dashed line indicates chance performance (50%).



Chapter 3: Olfactory Serial Probe Recognition in humans

Abstract

The serial probe recognition task is a useful comparative procedure as it allows for comparisons of list memory and related psychophysical functions across species. The SPR task yields a serial position function, which demonstrates the effects of proactive and retroactive interference on memory in form of primacy and recency effects (respectively). This procedure, widely used with visual and auditory, especially linguistic, stimuli, has seldom been used to test olfactory memory. Previous studies frequently, though not always, fail to demonstrate primacy effects in olfactory SPR tasks, though recency is almost always present. A key limitation of these studies is a failure to systematically manipulate the time between list presentation and test, referred to as probe delay. In comparative studies, increasing the length of the probe delay shifts the relative balance of proactive and retroactive interference, with longer delays leading to pronounced primacy effects and short delays show a strong recency effect. This finding is referred to as a recency to primacy shift with delay. In this study probe delay was systematically manipulated, starting with 15-s and up to 120-s in an SPR task with human participants. We found evidence of a strong recency effect during the shortest delay, which then dissipated at the longest delay. There was no effect of a primacy effect or a recency to primacy shift with delay; however, accuracy significantly improved for the first serial position as a probe delay increased.

Keywords: olfaction, memory, serial probe function, serial probe recognition, probe delay

Introduction

Memory in humans and animals has been tested under a variety of procedures. With animals, one of the most common methods is the delayed match-to-sample (dMTS) task (Lind et al., 2015). In the dMTS task, subjects are first presented with a sample item, before it is removed for a set delay period. After the delay, two (or more) items are presented, one of which is the same as the sample item while the other(s) is different. Participants or subjects in these experiments are rewarded for selecting the item that matches the sample. This procedure has been modified for different sensory modalities, including spatial, olfactory, auditory, taste, and visual variants. A procedure related to the dMTS is the serial probe recognition task, which has been used in humans and animals to measure list memory as well as effects of interference. As opposed to single item memory tasks like dMTS, list memory requires subjects to remember many items at once, rendering it memory for serially presented stimuli. Typically, tests of recall and recognition for lists produce a memory function called the serial position function (SPF). The classic SPF is defined by better memory for items earlier in the list, called the primacy effect, and for items at the end of the list, called the recency effect. Items falling in the middle of the list tend to be remembered more poorly than the items at the beginning or end of the list. When plotting the accuracy of remembered items in a given list as a function of list position (i.e., serial position), the SPF frequently takes on the form of a "U" with the higher points representing primacy and recency while the sagging middle shows the lower accuracy for the intervening items. List memory tasks, in particular the serial probe recognition (SPR) task, are ideal for tests of memory because they allow researchers to look at effects of interference on both long-term and working memory in a single session (Wright, 2006). For the comparative psychologist, the serial probe recognition task is adaptable for different species, and thus, across species comparisons can be made. Determining the functional relationships between

experimental parameters of SPR tasks and the effects these have on the shape of the memory curve provide information on how interference affects memory for items or events experienced as a series. Parameters such as list length, probe delay, inter-stimulus interval, and inter-trial interference can all affect the shape of the SPR function.

This chapter will discuss issues regarding proactive interference in list memory as well as how this pertains to issues of sensory modality, particularly olfaction. There is also a discussion on the differences in olfaction from the physical senses (touch, vision, audition) and the chemical senses in general. I will also outline an experiment to investigate the psychophysical functions of olfactory list learning in human participants. This experiment will account for some of the short-comings in previous attempts to explore olfactory list memory in humans, of which few exist. The experiment will also further elucidate the nature of proactive and retroactive interference in olfactory memory. Finally, I will discuss potential implications of olfactory psychophysics in the context of COVID-19.

Wright (2006) argues that SPR tasks are an ideal procedure for memory because, unlike other tasks, it is possible to see how proactive and retroactive interference interact in order to produce the classic primacy and recency effects found in SPR tasks. Tests of list memory across species have revealed general memory processes related to interference and the SPF. Sands and Wright (1980a) tested a single rhesus macaque monkey on the SPR task. The monkey had previously been trained on a same/different (S/D) discrimination task, where it had to report whether a probe item had been the same as or different than a sample item. The S/D procedure commonly used by Wright and colleagues (e.g., Wright and Katz 2006) is as follows: Subjects are initially presented with a sample stimulus before being presented with a single comparison stimulus displayed below the sample stimulus location. If the comparison item is the same as the

sample item, contact (e.g., pecking or touching) with the comparison stimulus is considered a correct response. If the comparison stimulus is different, then subjects make another response; they must make contact with a small white square next to the comparison stimulus location to be rewarded (humans are often given feedback instead of reward). This forms the basis of an SPR task in nonhumans by providing a learned behavior that can be adapted to test list memory by expanding the number of sample items. Essentially, the animals are first learning the SPR task with a 1-item list (i.e., an S/D task). With this training in place, experimenters can expand the lists by presenting more than one stimulus at the sample location (e.g., three stimuli at the sample location in a trial would be a 3-item list). In the Sands and Wright (1980a) study, the monkey, after acquisition of the S/D task, was presented with a series, or list, of sample images, either 10 or 20 images long. After a retention interval, a probe stimulus is presented. This could be one of the images from the list in same trials, or in a different trial, the probe would not have been present in the list. “Same” responses indicate that the probe item was in the list, and “different” responses indicate that the probe item was not in the list. With this procedure, researchers have conducted comparative studies on memory with variety of species, including rhesus macaques (Sands & Wright, 1980b; Castro, 1995), capuchins (Wright, 1999), pigeons (Wright et al., 1985), rats (Kesner & Novak 1982), and humans (Wright, 1989), including infants (Cornell & Bergstrom, 1983). Each of the cited examples employs some variant of the SPR task and demonstrates both primacy and recency effects, representing a qualitative similarity across species and human development, as well as indicating a general process of memory. By varying different parameters in these studies, researchers have found functional relationships between certain variables and the shape of the SPF. Of particular note for this chapter is the effect of time as a function of retention interval.

Temporal factors in the presentation of stimuli in SPR experiments greatly affect interference and the shape of the SPF (Wright et al., 1985). There are several opportunities in a typical SPR to manipulate time, including the time between the presentation of each stimulus in the list (i.e., the inter-stimulus interval: ISI), the time between trials (i.e., the inter-trial interval: ITI) as well as the time between list presentation and the probe item (probe delay or retention interval). Systematically varying probe delay can dramatically alter the shape of the SPF. Wright et al. (1985) illustrate this effect of probe delay by providing evidence of a dynamic, shifting SPF based on manipulations of probe delay across four species: capuchin monkeys, rhesus monkeys, humans, and pigeons. To ensure that testing environment and procedures were as uniform as possible between all species, humans and monkeys used the same apparatus while pigeons necessarily pecked at a screen in an operant chamber. The human and monkey apparatus was a lever that could move three directions: down, left, and right, like a "T." Pigeons pecked at two key lights with different colored discs that were either on the right side or left side of the chamber. Each list was four items long in this experiment. First, the four items were presented with a 0-s probe delay. That is, after subjects viewed the list, they were immediately given the probe test. Each species showed a similar SPF, where primacy was absent, but recency was prevalent. As the retention interval/probe delay increased, the SPF changed. At 1-second and 2-second delays for pigeons; 1-,2-, to 10-second delays for rhesus monkeys; 10-seconds for capuchins; and 10- to 60-second delays for humans, the SPFs were U-shaped, showing both primacy and recency effects. At the extreme end for each species (10, 30, and 100 seconds for pigeons, monkeys, and humans, respectively) the opposite pattern from the 0-s delay trials occurred. Recency effects disappeared for all species SPFs, and primacy effects were prominent. Figure 3.1 shows data from this study (figure is a colorized version from Wright et al., 2018) and

shows the shifting SPFs for each species. This is referred to as a recency to primacy shift with delay; the recency effect at 0-s delay shifts to a primacy effect with delay. This result suggests that each species' memory processes share some overlapping features. It provides evidence of qualitative similarities (each species showed the recency to primacy shift), yet it also shows quantitative differences (different retention intervals were required to cause the shift; pigeons showed the worst overall accuracy).

Interference theory can explain these results. Proactive interference and retroactive interference are two sources of forgetting or retrieval failure. Proactive interference (PI) occurs when memories for events preceding the present moment cause confusion or forgetting in the present moment. Retroactive interference (RI) is similar, but instead, memories from the present moment cause confusion and forgetting of past events. As such, PI and RI can explain forgetting (Wright, 2007) in the learning of lists, including the recency to primacy shift in Figure 3.1. The shape of the SPF depends on shifting effects of PI and RI. The first item in the list actively interferes with memory of the items following it, while the items at the end of the list interfere with items preceding it. With long enough list lengths, there is evidence of both primacy and recency effects occurring at the same time. In these procedures, there tends to be very low accuracy for recognizing items in the middle of the list due to the combined effect of PI and RI. Murdock (1962) demonstrated this by increasing the length of items in a list from 10 to 40. By the time participants were learning 40-item lists, the SPF became more pronounced with a small primacy effect, very poor performance for middle items, and strong recency effects. Accuracy for beginning and middle items decreased as a function of list length, but there was no difference in recalling the last stimulus of either 40-item or 10-item list. Figure 3.2 is taken from this study. Primacy reflects slower processes that need time to take an effect, such as rehearsal or

consolidation. Increasing opportunities for rehearsal tends to increase the strength of the primacy effect. However, as seen in figure 3.2, a longer list, which would allow for more rehearsal time for early items, does not result in a primacy effect but a more pronounced recency effect. This is due to the combined effects of retroactive interference of all the items that occur between the first stimulus and the probe delay. In addition to rehearsal or consolidation, another potential mechanism for the primacy effect is that increasing the time from the first stimulus to the probe period has the effect of making the first items more temporally distinct from the last items (Neath & Surprenant, 2002). Recency effects tend to be short lasting and reflect temporary or shorter-term memory processes, and therefore, are at their strongest with a 0-s probe delay. The primacy effects are at their strongest with longer delays (due to extra processing time) and shorter lists that reduce the effects of retroactive interference. These two concepts combine to determine the shape of the SPR as well as to cause the recency to primacy shift. At the 0-s delay, there is little to no time for slower processes, especially with short lists as in Wright et al. 1985.

Auditory list memory

More evidence of interference processes governing list memory comes from tests of the SPR across sensory modality. Wright (1999; 2002) found modality differences in monkeys tested on SPR with visual and auditory stimuli. Using the same procedure for both modalities, Wright tested two monkeys on auditory and visual SPR. An SPF was generated for both modalities at six different retention intervals (0-, 1-, 2-, 10-, 20-, and 30-second delays). Monkeys' SPF for auditory and visual stimuli were complete mirrors of each other. For auditory stimuli at zero seconds, there was a strong primacy effect but not recency effect. At 30-s delay, the opposite was true with a strong recency and a suppressed primacy effect. For visual stimuli at zero second delay, there was no primacy effect, but there was a recency effect. The opposite again held true

for the 30-s delay, such that there was a strong primacy effect but not a recency effect. Thus, manipulation of probe delay for auditory lists leads to a primacy to recency shift rather than a recency to primacy shift as seen in visual memory. This is a crucial finding, and it represents the best evidence against a mere memory strength account for the recency effect. When there is no probe, and therefore when memory should be strongest, there is no recency with auditory lists. An account for recency where the recency effect is solely attributed to the ease of retrieval from a working memory store cannot account for this, but an interference explanation, where we can assume different sensory modalities may have different interference effects due to the different physical properties of those modalities, can account for this effect (Wright, 2006). Thompson and Herman (1977) found only recency in dolphins tested on a 6-item auditory SPF, which may further suggest differences between species in auditory list memory. In humans, Mondor and Morin (2004) found primacy and recency effects when using an auditory suffix, which is a nonverbal sound that follows a to-be-remembered list. Suffix effects occur when an irrelevant cue or stimulus is presented during retention, and this typically results in recency reductions.

List Memory of Chemical Senses

Chemical senses involve olfaction and gustation as well as the ability to detect chemical irritants or toxins (e.g., trigeminal sensation or chemesthesis; Lundstrom et al. 2012; Stevenson, 2013). Relative to vision, less is known about the ways in which chemical stimuli are represented, let alone the existence of a dedicated working/short term memory system for odorants and tastants at all (White, 1998). A core issue is determining the ways in which odor perception is encoded in the brain. This is well known in vision, where light traveling at certain wavelengths is detected by photoreceptors, encoded into neural signals, and eventually form a variety of neural maps (e.g., retinotopic, ocular dominance, orientation, motion, and others;

Chklovskii & Koulakov, 2004; Swindale, 2000) and are processed further for spatial location and object recognition. The auditory cortex and somatosensory cortices are also arranged topographically (Saenz & Langers, 2014; Sanchez-Panchuelo et al. 2010). These maps are present in all mammals and represent a core mechanism for how the brain represents the physical world (Kaas, 1997). Olfaction represents a difficult problem with mapping because an olfactory map must somehow represent the discontinuous features of chemical space (Imai, Sakano, & Vosshall, 2010). There is evidence that the olfactory epithelium and olfactory bulbs do have stereotyped representations of specific odors, and these are represented in the olfactory bulb via spatial patterns of activity (Xu et al., 2000). This seems to correspond more to the position of the olfactory receptors in the olfactory mucosa, rather than any external quality of the odor space. The olfactory bulb is separated into different zones, each of which receives input from olfactory receptors that respond to an odors functional group (e.g., acidic, or alcoholic). Within each zone, olfactory bulb glomeruli responding to carbon chain length are organized linearly, such that information from olfactory receptors that have detection odors with similar carbon chain lengths will be received by glomeruli adjacent to each other. Therefore, it can be said that the spatial organization of the olfactory bulb is "chemotopic." Additional differences between olfaction and other senses includes a separate pathway for olfactory processing. Whereas all other sensory information is processed by the thalamus before being routed to neocortical areas, olfaction is, after early processing in the olfactory bulb, routed directly to the primary olfactory areas, including the pyriform and entorhinal cortices, amygdala, and parahippocampus (Lie et al., 2021). Finally, unlike taste, which in humans can be reduced to five distinct qualities (i.e., sweet, sour, salty, bitter, and umami) or color vision, which in humans can be reduced to the way three

photopigments and photoreceptors interact as color primaries, there is no similar construct–no odor primary–for olfaction, at least in terms of perception.

Daniel and Katz (2018) tested humans on an SPR task with taste stimuli. Participants had to taste a series of three liquids and then report whether a probe was the same as or different than one of the list liquids. Crucially, the probe delay interval was manipulated. Probes could occur 15, 30, 45, or 60 seconds later. Like with visual stimuli, this manipulation creates a recency to primacy shift. That this is similar to vision, yet apparently dissimilar to audition suggests that memory processes may be further dissociable. Not only are there different effects on recognition due to PI and RI, but they potentially interact with sensory modalities to produce different effects. In regard to olfactory list memory, only Reed (2000; described in detail below) consistently found both primacy and recency effects for olfaction, whereas other have found only a recency effect (Miles and Hodder, 2005). Reed (2000) suggests this could be due to the nature of the stimuli used in these experiments. For instance, the stimuli may have been too similar or too numerous, making PI very strong and suppressing recognition accuracy. It has been demonstrated (Cook et al., 1991; Wright et al., 1990) with human participants that it is difficult to find primacy effects with hard-to-name stimuli (e.g., complex kaleidoscopic images), which raises the question of to what extent studies of list memory in humans are testing verbal memory rather than the memory of a particular sensory modality. Additionally, there is evidence that easy-to-name odors are associated with prefrontal language areas of the brain while difficult-to-name odors are associated with increased and consistent activity in the primary olfactory cortex (Zelano et al., 2009). If accuracy in an olfactory recognition task depends on activation of prefrontal language areas, it is possible that subjects are not using olfactory cues much, if at all. Dual coding of olfactory information, that is, representing an odor by its smell or chemical

properties as well as verbal label, creates the same issue. The mere act of recognizing odors is controversial; some argue that odors are not objects in a perceptible sense at all, while others disagree (Millar, 2019). This suggests a possible confound in studies of olfactory memory; in order to actually recognize a stimulus, one may use verbal labels in addition to recognizing the odor itself or even in place of recognizing the odor at all. Recognizing something because it smells like an apple and produces the word 'apple' in one's mind is not the same as recognizing the smell of an apple on its own or smelling an apple and understanding that an apple exists in the moment. Dissociating olfactory recognition from the use of verbal labels is important in understanding the nature of olfaction, as it is possible that the verbal labels of the odors themselves is what shapes the SPF rather than recognition of individual odors (White and Treisman, 1997).

Previous olfactory SPR experiments

Reed (2000), borrowing from Neath (1993), used a procedure similar to the serial probe recognition task, where after a series of odors are presented, subjects must do a 2-alternative forced choice task (2-AFC) between a novel odor and a familiar odor from the list. In the first of Reed's experiments, participants were exposed to sets of five odors for a total of 3 seconds each. After each list, there was another 3-s delay before the recognition test, then a 5-s ITI before the next trial. Odors were seven essential oils. Each odor occurred approximately equally as often at each serial position, and there were 20 trials overall, four 2-AFC tests for each position. Results from this experiment demonstrated a classic serial position curve where primacy and recency effects drove down the accuracy of the middle position in terms of accuracy, relative to the first and last odors (~50% for position three vs 80 or 90% accuracy for positions one and five, respectively).

Miles and Hodder (2005) directly attempted to replicate Reed's (2000) results, citing the theretofore lack of evidence of the primacy effect using olfactory stimuli. In his study, Reed (2000) listed these odors as such: "Heartfelt," "White Musk," "Oceanus," "Vanilla," "Strawberry," "Ananya," and "Dewberry." Miles and Hodder (2005), purchasing odors from the same location, added "Potpourri" and "Spirit of Moonshine," and also replaced "Dewberry" with an odor called "Black Currant." In their first experiment, meant to directly replicate Reed's (2000) first experiment, Miles and Hodder (2005) failed to find a primacy effect. Over several follow-up experiments in that study, they found no primacy effect when increasing list length and no serial probe effect when decreasing ISI. Increasing list length strengthened the recency effect. When manipulating nameability, two new sets of odors were used. These were much more recognizable odors ("Lemon," Chocolate," "Coffee," "Banana," "Mixed Herbs," "Peppermint," and "Licorice"). However, it is not clear whether these labels were given to participants. These easier-to-name odors had the effect of flattening the SPF curve, eliminating primacy or recency. Using harder-to-name stimuli ("Stable/Horses," "Coconut," "Washday," "Gingerbread," "Pineapple," "Havana Cigar," and "Mahogany") produced another recency effect with no primacy effect. Verbal suppression and interleaving a suffix (presenting an irrelevant odor during ISI) consistently led to a recency effect but not a primacy effect.

Johnson and Miles (2009) compared modalities in an SPR task with olfactory, visual, and auditory stimuli in humans. For the olfactory stimuli, participants were able to smell a list of six odors for one second each. After a 3-second retention interval, participants were given an odor and had to state which position it was in the list. Odors could be pulled from a set of 54 liquid odors. The visual stimuli were similar, except they were 54 color faces of adult males with neutral expressions. Auditory stimuli were 54 pure tones presented for 1000 ms each, ranging

from 300 to 4,024 Hz. The olfactory component was similar to that used by Miles previously, except participants had to report where in the list the item occurred. This difference may account for the failure to find even a recency effect. The only modality to produce any effect was audition, and that only produced recency.

These previous studies have key limitations: the probe delays were not systematically manipulated, and there was a lack of control in the nameability or recognizability of the set of odors in the experiment. Probe delays need to be manipulated to show the specific delay length where recency to primacy shift could occur. For example, Wright et al. (1985) used delays of 0s, 10s, 60s, up to 100s (among others) in order to demonstrate a visual recency to primacy shift. Daniel and Katz (2018) used delays of 15-s, 30-s, 45-s, and 60-s for taste recency to primacy. Taste and olfaction are both chemical senses and are directly related during eating and drinking; perceived flavor is due to the interaction of odorants entering the nose retronasally from the esophagus and the taste of the food on the tastebuds. While it is possible that there is no capacity in the human memory system to produce robust and consistent olfactory primacy effects, it is also possible that the specific functional parameters have not been found. Systematically manipulating probe delay by increasing the length of those delays could reveal these functional characteristics of olfactory SPF. One cannot rule out the possibility of olfactory primacy effects unless the functional parameters of the SPF are manipulated. Using a range of probe delays is more likely to reveal the parameters necessary to observe olfactory primacy. Bromley and Doty (1995) found little to no drop off for olfactory memory after 40-s. Tests of list memory with delays shorter than that may fail to show primacy effects if there is still too much retroactive interference from items at the end of the list. If, after extensive manipulation of probe delay,

there still is no consistent primacy effect, then it may be true that there is no mechanism for olfactory primacy.

A second limitation is a lack of consistent control for the effects of verbalization. This proposed experiment would have participants rate dozens of odors to determine if they are easily recognizable and how nameable they are. Easier-to-name items can be rehearsed, which typically increases primacy effects. Previous research in our laboratory has used household spices and extracts as odors, instead of arbitrarily named scents one might find at a candle shop. Items like vanilla or orange extract are far more recognizable than "Heartfelt." While Miles and Hodder (2005) did use easier-to-name odors, it is possible that even that was not enough to provide a usable label. The length of the list (e.g., the number of items to study) could also be a factor in human olfaction. As mentioned above, increasing list length tends to increase recency and retroactive interference. Very strong RI could drive down early list performance, to a point. Using a shorter list, plus longer delays, could be enough to produce a recency to primacy shift. These varied results indicate a need to study not just the recognition of odors during serial probe studies but also in the form of simple match-to-sample experiments. The lack of replication of the primacy effect could reflect a fundamental aspect of olfactory processing and memory. Namely, that it is not as subject to primacy effects as other sensory modalities (e.g., taste, vision).

Impact of COVID-19

The ongoing COVID-19 pandemic has particular relevance to issues of olfaction, given how publicized olfactory-related symptoms have been. Post-viral anosmia is common with many viruses, not just COVID-19. With the pandemic, there has been a great deal of interest in anosmia as result of infection (Karamali et al., 2022). Many people who have recovered from the

COVID-19 virus report long-term olfactory dysfunction (OD). Loss of olfaction is a common symptom with viral upper respiratory infections (URI), typically due to nasal inflammation, swelling of mucous glands, and lack of airflow to olfactory system. These are generally short lasting however, and long-term loss of olfaction might suggest viral damage directly to the olfactory system (Soler et al., 2020). We will provide a questionnaire on COVID, so the relationship between COVID and list memory performance can be examined. Anosmia, the total loss of smell, is a one of the more common symptoms of COVID-19 (Najafloo, et al., 2021). Ho et al. (2021) found that recovered COVID-19 patients performed worse on a "Sniffin Sticks" test (SST), a 12-item olfactory discrimination test, than did healthy controls. Vandersteen et al. (2022) similarly found the SST to be an effective screening tool for post-COVID anosmia. Di Stadio et al. (2022) found that sufferers from so-called "Long COVID" were more likely to have severe OD when also suffering from long-term cognitive impairment such as mental clouding (often referred to as brain fog) and headaches, suggesting a shared neuroinflammatory mechanism. Alternatively, it could be that mental clouding and headaches impair perception of olfactory stimuli as opposed to the mere act of smelling. Interestingly, Hannum et al. (2020), in a review comparing objective to subjective measures of olfactory loss following COVID-19 infection found that providing object measures not only provided a more accurate test of olfactory but also identified a greater prevalence of olfactory loss than self-report. Including a COVID-19 screening questionnaire for OD could yield interesting results for this study in terms of PI and the SPF. Surveying participants for COVID-19 infection history and self-reports of loss of smell and comparing performance on list memory (as well as other psychophysical measures of olfaction) could reveal important information for how COVID-19 affects olfactory systems.

Experiments

There are two experiments discussed in this chapter. The first experiment is a dMTS task followed by a series of Likert-scale assessments of each odor. Participants rated each odor according to intensity, pleasantness, familiarity, and verbalizability. Ratings of odors from this first experiment were used to select a standard set of odors that are roughly equivalent in each measure for Experiment 2. The second experiment was an olfactory serial probe recognition study that has a similar set up to previous experiments (Reed, 2000; Miles and Hodder, 2005). This experiment was designed to address the core limitations of previous attempts to examine the psychophysical relationship between olfaction and the SPF, which is the lack of systematic variation in probe delay. As discussed, previous studies found at most limited evidence of the primacy effect (Reed, 2000), and in some cases no SPF at all (Miles and Hodder, 2005). The following factors were manipulated or controlled: probe delay (use of different probe delay lengths), relative distinctiveness/recognizability of the odors (use of odors that are roughly equivalent based on evaluations in Experiment 1), and verbal labelling (via verbal suppression). Recency effects were expected to be evident during shorter probe delays. If increasing the probe delay has an effect, it may produce primacy effects, especially at longer probe delays, under which circumstances we expect to find evidence of a recency to primacy shift. Finally, having all participants take part in a verbal suppression procedure was intended to mitigate the role of verbal labelling in olfactory memory processes.

Methods

Experiment 1: Initial preference testing and dMTS

The same odors as described in chapter two were used with minor variation. Specifically, tobacco was replaced with orange extract, and apple was replaced by dried bay leaves. These changes were made as the original sources of these odors were no longer available. Daniel and

Katz (2018) started their taste SPR study with a recognition task. The purpose of the task was to determine how flavors were temporarily retained in memory during a probe delay. They collected reports from the participants on how the hedonic value, intensity, and recognizability of each taste to determine whether this had an additional effect on memory. Zelano et al. (2009) found in an olfactory recognition task that nameability affected performance. Hence, it is important to determine to what extent each odor can affect memory on these dimensions. Additionally, it presents an opportunity to explore the comparative nature of these odors as well as proactive interference. The recognition task was a dMTS task, similar to the one described in Chapter 2. Along with the dMTS task, participants rated each odor on a 0 – 100-point scale in terms of intensity (how easy it is to detect), hedonic value (how pleasant it is to smell), verbalizability (how easy it is to describe), and familiarity (how often they encounter this odor). These ratings were used to select a set of odors for the list memory experiment that are roughly equivalent on each value.

Participants

30 undergraduate students (26 female, 4 male) age 18-23 were recruited from Auburn University's SONA recruitment system. Participants were offered course credit for participation. 12 participants reported having had COVID-19 at least once.

Stimuli and Apparatus

Timing and scoring for each trial used PsychoPy-2022.2.0. The stimulus set consisted of 48 different odors. All stimuli were presented in a small white vial that had an odorized cotton round placed inside. The cotton rounds were stored in a glass mason jar that had the odorant substance at the bottom, with cotton rounds stacked inside. Each week, experimenters removed

the odorized cotton round from the previous session and replaced it with a fresh cotton round. Fresh cotton round pads were always selected from the top of the stack in the jar. The plastic vials are white and have no discernible markings on the outside. Some substances, such as ground spices, could provide a visual cue to participants. Therefore, all participants were instructed not to look into the vials while smelling. Table 3.1 is a list of all odors in the experiment.

Procedure

dMTS task

Participants sat at a computer that coordinated the experiment using PsychoPy-2022.2.0 software. After reading instructions, the participants began the dMTS procedure. Figure 3.3 is a schematic of the progression of a single trial. There were 48 trials, such that each odor served as both sample and incorrect comparison. Each trial began with a ready screen (a screen with instructions to press the spacebar when ready), followed by instructions for participants to smell the sample odor and return it to the experimenter. After the delay, the experimenter handed two odors to the participant, one of which contained an odorized cotton round that matched the odor of the sample, and one that did not match. The order was counterbalanced, such that the correct odor was presented first or second equally across trials. There was an opaque, white divider that kept the subject and experimenter out of view of each other. The odors were delivered via a foam tray with cut-outs for each vial. Each cut-out also has a label, either 1 or 2. Participants pressed "1" on a keyboard when odor 1 matched the sample, or "2" if odor 2 matched. Participants received feedback after each response via onscreen popup, either "CORRECT" for correct responses, and "INCORRECT" for incorrect responses. There was a 15-s ITI.

Odor Ratings

After the dMTS task, participants used the computer mouse to respond along a scale number line, starting with zero and ending with 100 (cf., Daniel & Katz, 2018). An instruction screen on the computer told the participants how to rate each odor. For each odor, participants rated it on a scale from 0 to 100. A zero-rating on the intensity scale indicated the participant can barely smell the odor at all, and a 100-rating means the smell was overwhelming. For the hedonic value, zero-rating means the participant hated the odor, while 100-rating means they loved the odor. A zero-rating on verbalizability means the participant could think of no words to describe the odor, while a 100-rating means they could easily think of a word to describe the odor. For the familiarity value, a 100-rating meant they encountered the odor nearly every day, while the zero-rating meant they had never encountered the odor before. They were also asked if they wanted to share out loud a word or words to describe the odor. After the ratings task, participants were debriefed and allowed to ask questions regarding the study.

Results and Discussion

dMTS

Data were analyzed in R (version 4.3). There was no difference between participants who reported have had previously had COVID-19 (M = 95.41, SD = 3.65), and those who had not (M = 93.05, SD = 5.15), $t(28) = -1.32$, p = .197, so all data are collapsed over COVID-19 history. A one-sample t-test was conducted to determine whether accuracy was greater than chance performance, (i.e., 50% correct) in the dMTS task. Accuracy was calculated as a percent correct for each participant. The t-test revealed that participants were able to accurately recognize (M = 93.89, SD = 4.61) the sample odor after a 30-s delay at a level significantly greater than chance, $t(29) = 52.172$, $p < .0001$, $d = 9.52$. The results indicate that memory in this task is not limited to intervals less than 30-s.

Odor ratings

27 of 30 participants completed ratings. Two participants' data were dropped for not completing each rating. If one rating were to be skipped, it would be impossible to accurately assign successive ratings to the correct odor. Another participant's data was lost due to a technical error. Ratings from the odor ratings task were mean averaged across participants for each measure. Microsoft Excel was used to apply a color scheme for all odors in each measure. The highest score in each measure was assigned the darkest green, while the lowest score the darkest red. Pure yellow represents the 50^{th} percentile of the ratings. Colors with any red were below the 50^{th} percentile and ratings with green were above the 50^{th} percentile. These ratings were relative to other ratings within a single rating. For example, Cinnamon and Garlic were both coded with dark green as the two most intense odors, with ratings of 88.28and 89.40, respectively. The highest rated odor in terms of verbalizability was orange, with a rating of 75.20. All of these ratings were coded as dark green as the high end of the average range of ratings within that single category. Figure 3.4 shows this color-coded chart. Additionally, we ran a series of Pearson product-moment correlations between average odor ratings and participant accuracy to determine whether any particular odor quality, whether in terms of hedonic value, verbalizability, intensity, or recognizability, is associated with improved memory in the dMTS task. None of the correlations survived Bonferroni correction for multiple comparisons. Another series of correlations between each odor quality found each quality was significantly correlated ($ps < .000$) with each other rating. Table 3.2 shows a matrix of these correlations. Familiarity and verbalizability in particular were very highly correlated, with a correlation coefficient of .94). Regardless of whether participants were able to accurately verbalize the odor, their reported ease of doing so was related to how familiar the odor was. Perhaps past experience, or the perception

of past experience, drives verbalizability. While still significant, intensity and pleasantness had the lowest correlation coefficient of .50. Intense odors were often perceived as pleasant; however, some were not.

Selection of odors for Experiment 2 took these ratings into consideration. Odors that were most similar in relative rating color-coding were selected. These odors were blackberry, butter, caramel, clove, lime, orange, peach, pina colada, raspberry, rosemary, strawberry, and watermelon. Odors that varied significantly in one rating relative to the other ratings were not included. For example, garlic was rated highly in intensity, verbalizability, and familiarity, but relatively low on pleasantness. This profile was unique to garlic, and potentially made it more distinctive. Odors like this were avoided as they may evoke a von Restorff-like effect where an odor might be more distinct if it varies across each measure in a unique manner. More distinctive stimuli may evoke greater interference over other items. In future studies, other approaches to selecting odors for olfactory studies should be explored. This could include collecting much larger data sets (i.e., more odors and more participants) to perform more advanced statistics such as cluster analysis, or including additional odor characteristics, such as how irritating the odor is (Moss et al., 2016).

These results indicate that participants' memory for odors after a 30-s delay was relatively high, corroborating similar evidence (Zelano et al., 2009); yet, in this case, there was no possibility of proactive interference on recognition as each trial was a novel pairing of odors, and each participant was tested for a single session. This represents a dMTS task for odors that is completely free of within-session proactive interference. For Experiment 2, these results indicate that using a 30-s probe delay length would not cause participants to be unable to complete the task for delay lengths $\leq$ 30-s.

Experiment 2: Serial probe recognition

Experiment 2 tested participants on the SPR task using a 3-item list, in a between-groups design with four probe delays to determine whether a recency to primacy shift occurs with increased delay. Assuming these probe delay lengths are sufficient, a recency effect will be evident at the shortest delay, and primacy effects will be dependent on whether longer delays are sufficient to produce it. A 3-item list was utilized over longer lists for a number of reasons. Daniel and Katz (2018) used a 3-item and found the recency to primacy shift with extended delays, demonstrating the validity of the list length. Further, while very long lists yield primacy effects (though whether this is true for olfaction is unknown), a 3-item list allowed for the development of the procedure without concern for the length of each trial. As the length of each trial is at least partially determined by how quickly the participant returns each odor the experimenter, each additional odor adds some variation to the total time of each trial. In the current experiment, these differences could add several seconds to each trial, but as they compound there could be 30-60s difference between participants depending on the length of the list. An olfactometer would allow for precise control of each odor, which would better allow us to explore the effects of a long list of odors. Further, as the length of the list increases so too does the session length, creating a tradeoff between probe delay and list length. The 120-s sessions lasted over 80 minute, and even a 6-item list would add several minutes to that time. Hence, a 3-item list was chosen.

Participants

Participants were 40 Auburn University undergraduate students (33 female; 7 male) aged 18-23, recruited through the Department of Psychological Sciences Sona Systems pool of participants. 22 reported having had COVID-19 at least once.

Stimuli and Apparatus

This study used the same computer and PsychoPy-2022.2.0 as in Experiment 1 for timing and data collection. Data from the ratings task in Experiment 1 were used to construct a stimulus set of 12 odors for this experiment. These odors were blackberry, butter, caramel, clove, lime, orange, peach, piña colada, raspberry, rosemary, strawberry, and watermelon. The stimuli were odorized cotton round pads stored in white plastic vials, as in Experiment 1.

Procedure

Participants were seated at a computer that coordinated the experiment, just like in Experiment 1. On the screen were instructions describing how to respond, as in Experiment 1. As in Experiment 1, a divider was used to block the experimenter from the view of the participant. Instead of smelling one odor, however, each participant smelled three odors (i.e., the list) at the beginning of each trial, and a final odor after the delay period. Before each trial was a ready screen, which instructed the participant to press the spacebar when ready to start each trial. At the start of each trial, the experimenter handed over each of the three bottles one at a time. These bottles were each stuffed with a cotton round that had been scented with the olfactory stimuli at least 24-48 hours earlier. Cotton rounds were replaced at least once a week. This interval was chosen because the quality of the odors changed as a function of time. If the stimulus orange extract was prepared less than 24 hours prior to test, some tended to smell more like the extraction liquid (e.g., alcohol) rather than the extracted substance (e.g., orange). The bottles were white, identical, and otherwise nondescript, reducing visual information. Each odor presentation lasted for approximately two seconds where participants were instructed to smell each odor for about two seconds (one deep breath in and out) and pass it back to the experimenter, followed by a 5-s ISI. Participants waited through one of four probe delays, 15 s,

30 s, 60 s, and 120 s. During the delay, participants repeated aloud the word “the” once per second for the duration of the delay period. Participants that repeated “the” too slowly or too quickly were reminded and asked to keep to the rhythm. The verbal suppression procedure is intended to reduce the ability of individuals to apply a verbal label to olfactory stimuli. If measures are not taken to reduce the potential use of verbal labels, then it is not possible to know whether the results reflect olfactory memory or memory for the verbal label associated with each odor.

After the delay, the participants were presented with a single probe odor. The probe stimulus either matches one of the list items (i.e., same trials), or it does not (i.e., different trials). Same responses were keyed as a “1”, while different responses are keyed as a “2”. Figure 3.4 shows a schematic of the trial progression. Each session consisted of 24 trials, 12 same and 12 different. The 12 odors were counterbalanced so each odor occurs equally as a same and different probe choice. Within same trials, we counterbalanced list position such that the test stimulus matched the odor in each serial position four times each session. Additionally, each odor occurred six times as a sample list odor.

Results

Data were analyzed in R (version 4.3) using a generalized linear mixed-effects model (GLMM), with a binomial family distribution and covid history as a random effect of participant (lme4 package; Bates et al., 2015b). Accuracy was calculated as the probability of correctly answering “same” or different” for each subject at each level of the experiment. Accuracy was a function of both position (1, 2, 3), delay (15 s, 30 s, 60 s, 120 s), COVID history (yes or no) and a delay x position interaction. Sex was not included due to the relative lack of male participants. Participant ID was included as a random effect. As COVID effects might vary randomly based

on the individual infected, the initial model included COVID as a random effect nested within participant ID. Using ANOVA, this model was contrasted with a simpler model, where the random effect was only the intercept of participant ID, and COVID was only a factor in the model. The ANOVA was not significant, suggesting that the more complex model (with participant nested within COVID) does not explain more variance than the simple model. Including COVID as a factor led to convergence warnings and singular fit issues, likely due to model overfitting. An additional ANOVA to compare the models found no significant difference between models that included covid as a covariate. Therefore, removing the COVID factor allowed for the primary analysis to best address the theoretical issue at hand (that of primacy and recency in an olfactory SPR task), as well as avoid issues of model overfitting (Barr et al., 2013; Bates et al. 2015a; Matuschek et al., 2017). The final model was GLMM: accuracy ~ position + delay + position * delay + (1| Participant ID).

Figure 3.5 shows the relationship between mean accuracy at each serial position as a function of delay. Overall, accuracy was high across all conditions. Focusing on same trials, there was an interaction between delay and serial position (z = -2.11, p = .022, OR = .99, 95% CL = [.98, .99]). For serial position one, accuracy improved as delay increased. The opposite was true of position three, where accuracy decreased as delay increased. There was no effect of delay at position two. There were no significant differences in accuracy between each serial position when controlling for the effect of delay for position one (M = 77.50%, SE = 3.44), position two (M = 81.88%, SE = 3.47), or position three (M = 80.00%, SE = 3.6; GLMMs: ps > .1). The main effect of delay was significant (z = 2.015, p = .044, OR = 1.01, 95% CL = [1, 1.02]), such that as the delay increased there as an increase in accuracy. The difference between the effects of delay

at serial positions one and two and between positions two and three were not significant (GLMM: *p*s > .06).

Post-hoc contrasts were made using the emmeans package (Lenth, 2023) in R. These contrasts specifically compared the accuracy of position one at 15 s and 120 s to the accuracy of position three at 15 s and 120 s. At 15 s, there was a significant difference in accuracy between position one and three (z = -2.084, p = .0372). This difference is associated with a 27.5%-point increase in accuracy for position three. At 120 s, there was a 10.5% increase in accuracy for position one over position three; however, this was not a significant difference (z = 1.42, p = .157). Two more contrasts compared the accuracy of serial position one at the 15-s delay to the 120-s delay, as well as position three at 15-s and 120-s delays. For position one, there was a significant 25.5% increase in accuracy at the 120-s delay over 15-s delay (z = -2.051, p = .04). For position three, accuracy was 15% higher in the 15-s delay condition relative to the 120-s delay condition, but this difference was not significant (z = -1.39, p = .165). A recency to primacy shift would have been confirmed by a significant increase in accuracy for position one as a function of delay, as well as a significant decrease in accuracy for position three as delay increases. The significant increase in accuracy at position three over position one in the 15-s delay condition indicates a recency effect, while the significant increase accuracy at position one as delay increases suggests a recovery from the recency effect. The lack of a significant decrease in accuracy at position three between the 15-s and 120-s delays indicates that a recency to primacy shift with delay was not found.

We also compared the difference in accuracy between same and different trials. There was a significant difference between accuracy on same trials (M = 79.38%, SE = 2.05) over different trials (M = 70.00%, SE = 2.23). An additional GLMM compared the effects of trial type

(i.e., same or different) and delay on accuracy, with a delay * trial type interaction and with participant ID as a random effect. There was no interaction effect, so we dropped it to compare both main effects of delay and trial type separately. There was a significant effect of trial type (GLMM: $z = 3.34$, $p < .001$; $OR = 1.66$, 95% CL = 1.23, 2.233). There was no effect of delay (GLMM: $z = -.056$, $p = .59$).

Finally, we compared the effects of COVID on overall accuracy via GLMM with COVID history (yes or no according to self-report), delay (15 s, 30 s, 60 s, and 120 s), and a COVID history * delay interaction as fixed effects, with a random effect of participant ID. The interaction was not significant, so it was dropped in favor of a simpler model that only had the main effects and random effect term. Neither of these were significant (GLMM: $ps > .1$).

These results indicate that memory for odors in the SPR task depends on both the duration of the probe delay and the order in which the odors are presented. As delay length increased, we found a weakening of the recency effect, as well as a strengthening memory for the first item in the list of odors. However, this trend was not sufficient to produce a complete recency to primacy shift effect.

Discussion

These results are mixed regarding a recency to primacy shift. There was a clear recency effect at the shortest delay, such that accuracy for the third position was 27.5%-points greater than accuracy for the first position. Accuracy at position three decreases as a function of delay, down by 15% from 90% at the 120-s delay. However, this was not a significant difference. Accuracy for position one increased by 25% with delay, from 62.5% at the 15-s delay, to 87.5% at the 120-s delay. This indicates that the RI from the recency effect dissipated over the delay,

but this was not a significant effect of a primacy effect. There are two major explanations for these findings: interference theory and temporal distinctiveness.

Interference theory

Interference theory suggests that the shape of the SPF is due to competing effects of proactive and retroactive interference. Within a list of items, recency occurs when RI is stronger, and primacy occurs when PI is high. The commonly found U-shaped function is due to the suppression of memory for items in the middle of the list due to the effects of both PI and RI, and occurs when these two effects are both present, reducing memory for the middle items. Manipulating factors such as probe delay length can produce linear SPFs, indicating much stronger RI (at shorter delays) or PI (at longer delays). Such findings are common with visual stimuli, but unclear for olfactory stimuli. While previous studies have found evidence of olfactory PI and RI in humans outside of the SPR procedure (Köster et al., 2002), the results of tasks that use serially presented lists is mixed. The current study, along with other studies on olfactory PI (e.g., Reed, 2000), demonstrate that a mechanism for the primacy effect may exist for olfactory memory (i.e., proactive interference), but also that certain methodological approaches must be considered (i.e., sufficient probe delay length). Reed (2000) provided the only example that we can find of primacy in olfactory memory in humans, while Miles et al. (2005) provide evidence against it. In the current study the trend towards primacy at the 120-s interval suggests that a fully-powered study may be sufficient in producing a primacy effect. Additionally, a longer list may have shown the suppression in accuracy of middle items that come from both recency and primacy.

The present study did not demonstrate a recency to primacy shift: although the significant recency effect at the shortest probe delay was not evident at longer intervals, no

significant primacy effect emerged at longer delays. This could be due to using a sample size that was powerful enough to detect effects in the full model, yet not powerful enough to detect more granular effects. For example, there were only 40 observations for each serial position at a particular delay length (i.e., each of the 10 participants in each condition had only four trials where the test stimulus matched the first item). A larger sample size, or longer session, may have the power necessary to show the recency to primacy shift. Additionally, it is possible that using more extreme delay lengths would have yielded a stronger effect. These specific delay lengths, while chosen based on previous literature, may not have been sufficient to completely reduce the recency effect, and a longer delay should theoretically reduce the effects of recency while further increasing the primacy effect. The delay lengths of the current experiment may have been enough only to demonstrate a recovery from the recency effect, but not a full primacy effect.

Temporal distinctiveness

The results of the current experiment can also be explained by the relative distinctiveness of each stimulus as a function of time in each trial. Distinctiveness is a quantitative measure of how distinct a single stimulus is relative to all other stimuli in a particular grouping (Murdock, 1960). This theory suggests that the SPF, including the recency to primacy shift, is due to a change in the relative distinctiveness of stimuli in a list, where items that are more distinct in a list are easier to remember, relative to other items (Knoedler et al., 1999). Distinctiveness is often physical, such as presenting a list of to be remembered numbers, one of which is red while the others are black. The red item would be more distinctive, and therefore easier to remember. In SPF tasks, researchers often attempt to use stimuli that are as equivalent as possible across physical characteristics in order to minimize this effect of distinctiveness. However, an item could be distinct temporally as well as physically. In SPR tasks, items are presented serially with

both interstimulus intervals and probe delays spacing out each stimulus in a trial. Neath and Surprenant (2003) explain temporal distinctiveness values can be calculated for each stimulus in a list to determine which are most distinct. Typically, as the total time in a trial increases across ISI and probe delay, primacy increases while recency decreases as a function of relative distinctiveness. At shorter delays, or when there is no probe delay, recency is stronger. The relative distinctiveness of each item in a to-be-remembered list is calculated by taking the log of the total time (in seconds) of each ISI that occurs after the stimulus, in addition to the probe delay duration. Each stimulus will have an individual temporal value based on the ISI and probe delay, which then undergoes a log transformation. Taking the absolute value of the summed difference between each stimulus' log temporal value gives the distinctiveness value. This can be normalized to each stimulus set by dividing the distinctiveness value of a single stimulus by the sum of all distinctiveness values. Such normalization results in the last item in a list with greater distinctiveness than items earlier in the list at short delays, while as the delay increases the first item in the list becomes more distinct. Memory for a particular stimulus would improve monotonically as the distinctiveness of that item increases.

Applied to the current study, it is possible that at the shortest delay, the third item in the list is much more distinctive than any previous item. As the delay increases in length, the first item becomes more distinct. However, the third item at the 120-s delay is still relatively distinct, accounting for the nonsignificant decrease in accurate recognition. The significant change in accuracy seen in the current experiment could be due to an increase in distinctiveness. When comparing the temporal distinctiveness values derived from the current experiment, serial position one at 15-s delay yields a distinctiveness value of .74, while at 120-s this decreases to .119. The distinctiveness value for position three similarly decreases from .8 to .121. At the 15-s

delay, the significant recency effect could be due to the .06 advantage that the third item has in distinctiveness. The difference in distinctiveness between position one and three at the 120-s delay is down to .002, which might explain why there is a recovery from recency, while not necessarily a recency to primacy shift.

While interference theory and relative distinctiveness can explain these results, the confidence with which we can attribute the results of the current study to olfactory memory only depends on how well the verbal suppression procedure actually suppressed verbal activity during the probe delay. All participants were tasked with a verbal suppression procedure, which was intended to reduce the possibility of verbally encoding each odor. Using verbal codes would allow for the use of verbal labels for the recognition test rather than the odor itself. We debriefed each participant at the end of each session and asked about any strategies they used during the test phase of each trial. Almost all participants indicated they were able to use a verbal label they assigned to each odor, regardless of the actual odor identity. As participants only had to remember three odors on each trial, specific labels did not matter, so long as they were memorable. Others described intricate and ad-hoc mnemonic aids, such as tracing unique patterns on their leg during the suppression period. This represents a problem in interpreting these results, as the verbal suppression procedure is intended to decrease the potential for participants to use a verbal code or mnemonic aids that they can rehearse during the probe delay phase of each trial. If this did not work, or only worked in part, then it is difficult to determine to what extent these results reflect odor memory, verbal memory, the participants' ability to develop mnemonic aids, or some combination of these.

The issue of verbal suppression also affects the interpretation of other analyses. For example, the significant effect of the trial type analysis was unexpected. This suggests that there

was some factor that biased the data towards same trials. One possibility is that participants were able to use verbal labels despite the verbal suppression procedure. If these labels were broad and imprecise, two odors that could have the same label (e.g., lime and orange labelled as citrus) would bias participants towards a same response even on different trials. For example, if the list of odors were lemon, butter, and clove, and the different test stimulus was lime, a code of "citrus" for lemon would be true of both lemon and lime, leading to worse accuracy on different trials. An additional explanation is response bias. Kanter and Lindsay (2012) found that some individuals have a response bias in recognition tasks, generally being more likely to give either a "yes" (same in the current study) or "no" response. It is possible that the sample for the current study was composed of more individuals with a "yes" bias.

While there was no effect of COVID-19 history across any analysis, the failure of the verbal suppression task again prevents clear conclusions. While these results could indicate that the effects of COVID-19 are separate from processes of olfactory detection and memory involved in the serial probe recognition task, that is not necessarily the case. Alternatively, as participants were able to use verbal codes despite the verbal suppression procedure, these results may reflect verbal memory instead of olfactory memory. If so, then the study does not answer questions regarding COVID-19 and olfactory memory.

Future directions

It is vital to understand the role of verbal labelling in olfactory research. Past research has indicated that verbal labels of odors can play a role in the recognition of odor memories. Rabin (1988) found that participants trained to use labels for an olfactory discrimination task performed better than those who did not receive such training. Annett and Leslie (1996) found that verbal suppression tends to reduce odor recognition accuracy as a function of the difficulty of the

suppression task. Perhaps the specific verbal suppression task used in this study was too easy and did not sufficiently disrupt verbal coding.

Croijmans et al. (2020) examined the effects of verbal suppression on recognition of wine varietals and odors (some wine-related) by both wine experts and novices. The verbal suppression procedure required participants to remember a sequence of numbers, which varied in length based on individual working memory assessments. Wine experts' recognition memory for wine and wine-related odors was not affected by the verbal suppression, suggesting there is no verbal mediation once expertise is acquired. This suggests that under certain circumstances, verbal suppression can have an effect, but these circumstances do not seem to be well known. Future studies should be designed to uncover functional characteristics of verbal suppression. Developing an ideal procedure for verbal suppression would allow for better use of the procedure in order to isolate certain memory processes, as well as show how verbal labels and memory are related. Replicating the current study while incorporating Croijman et al.'s verbal suppression procedure would allow us to better understand the extent to which our results are due to verbal encoding along with olfactory encoding. A verbal suppression task can be validated by comparing accuracy in a suppression condition to a no suppression condition, as well as by thoroughly interviewing participants afterwards.

Once a validated and tested verbal suppression procedure has been developed, follow-up studies can be developed to uncover additional functional characteristics for olfactory memory in the SPR task. For example, increasing ISI tends to strengthen the primacy effect, while increasing list length tends to increase RI, producing a more pronounced recency effect.

General Discussion

The experiments described in this chapter contribute to the scientific literature on olfactory memory in humans. In Experiment 1, participants demonstrated a high level of accuracy in a dMTS task over a 30-s delay. In Experiment 2, the effects of a longer delay lengths on memory for lists of odors in a serial probe recognition task were examined. We found evidence of a recency effect, which dissipated with delay, such that accuracy for serial position 1 increased significantly in the 120-s condition. However, there was no evidence of a complete recency to primacy shift. Follow-up studies might use an even longer delay as well as a larger sample size to achieve a recency to primacy shift. Manipulating list length may also reveal changes in the SPF consistent with a recency to primacy shift. The failure of the verbal suppression task to adequately suppress verbal labelling or the creation of mnemonic aids further suggests the need to replicate and expand on these studies with procedures that have been demonstrated to interfere with the ability to give verbal codes to olfactory stimuli.

Additional studies could address the generalizability of the current experiments. First, there were very few male participants in the study; 57 out of 70 participants across both studies were female. Past research on olfaction has found a small but consistent sex difference (favoring females) across olfactory tasks (Sorokowski et al., 2019). Whether these would be detectable in an SPR task with a robust sample size is unknown. Possible differences may be that males show worse overall accuracy but no differences in the effects of interference. Second, subjects were undergraduate students between the ages of 18-23, which limits generalizations based on age. However, this was by design. The effects of age, especially age-related diseases such as Alzheimer's, on olfaction is complicated and warrants extensive research dedicated to that issue alone.

Another limitation that can be addressed in future studies is to provide a more exhaustive screening questionnaire to participants. For example, people who currently smoke are more likely to suffer from olfactory dysfunction (Ajmani et al., 2017). Electronic cigarette usage may have a similar effect. Other factors, such as time of day and time since last meal eaten are also possible items to include, as many odors were food-related (e.g., peanut butter). Satiety and circadian state can affect odor perception (Shanahan & Kahnt, 2022).

Comparative Implications

Adapting the olfactory SPR procedure to other animals would be especially interesting and vital to understanding olfactory memory in other species. Reed (1991) found evidence of primacy and recency in rats using olfactory stimuli in a radial arm maze. However, this study has been criticized (Gaffan & Gaffan, 1992) for having insufficient variance given the number of observations in the study (cf. Simonsohn, 2013 for an explanation of how this may indicate data fabrication). Other than Reed et al.'s (1991) study, there have been few studies that look at olfactory recognition memory in a manner that allows for the examination of PI and RI at once. Dogs would be an interesting subject for these studies as they are relied on for their sense of smell in service roles, such as explosive detection dogs. Dogs are often trained on a specific target odor in a controlled environment. However, real world scenarios would present multiple odors at once to dogs, some of which may be relevant or similar to target odors. Understanding how experiencing multiple relevant odors at once affects dog memory is important for efficiency in live detection situations. Incorporating this information for training purposes could improve training and success for working dogs (Cobb et al., 2015).

Conclusion

The experiments in this chapter explored olfactory recognition memory. Unlike other senses, much is unknown about the way olfaction is represented and stored as memories. Experiment 1 demonstrated that human memory for odors persists for at least 30 s. Participants also rated each odor on a several dimensions. These ratings were used to create the set of odors for the second experiment. In Experiment 2, participants completed an olfactory variant of the serial probe recognition task. This experiment expanded on past research (Reed, 2000; Miles & Hodder, 2005), by incorporating longer probe delays. In other studies (Daniel & Katz, 2018; Knoedler et al., 1999; Wright et al., 1985), increasing the probe delay duration shifts the shape of the SPF, from recency dominant at short delays to primacy dominant at long delays, referred to as a recency to primacy shift with delay. The current study replicated the recency effect, and while not completely producing a primacy effect, there was a strong increase in the memory for the first odor in the list at the longest delay, suggesting that there was an increase in proactive interference that was sufficient in strength to reduce the recency effect, but not quite strong enough for a primacy effect. These results suggest that the existence and prevalence of primacy and recency effects depends on the methodology, in this case probe delay duration. However, a major caveat to these results is that nearly all participants report the use of verbal labels or mnemonic aids in the SPR task. This renders straightforward interpretation of the results difficult and necessitates follow-up studies.

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Table 3.1

List of all odors used in both experiments. Note, bay and orange replace apple and tobacco from the experiments in chapter 2. All odors comprised the stimulus set for Experiment 1, while the odors for experiment 2 were blackberry, butter, caramel, clove, lime, orange, peach, piña colada, raspberry, rosemary, strawberry, and watermelon.

Allspice	Butter	Clove	Garlic	Parsley	Rosemary
Almond	Butterscotch	Coffee	Lemon	Peach	Savory
Amaretto	Caramel	Coriander	Lime	Peanut butter	Strawberry
Anise	Carob	Cotton candy	Maple	Pecan	Sumac
Apricot	Chamomile	Eggnog	Marshmallow	Piña colada	Tangerine
Bay	Champagne	English toffee	Mustard	Pineapple	Thyme
Blackberry	Cherry	Fennel	Orange	Raspberry	Turmeric
Blueberry	Cinnamon	Fenugreek	Oregano	Root beer	Watermelon

Table 3.2

Correlation table for each odor ratings. All ratings are significantly correlated, ps <. 0001, (denoted by asterisks)

	Intensity	Verbalizability	Pleasantness	Familiarity
Intensity	1	0.87***	0.5***	0.81***
Verbalizability	0.87***	1	0.75***	0.94***
Pleasantness	0.5***	0.75***	1	0.78***
Familiarity	0.81***	0.94***	0.78***	1

Figure 3.1

From Wright et al. 2018. Pigeons, rhesus and capuchin monkeys, and humans learned a 4-item SPR task. Difficulty was modulated to bring human performance more in line with pigeon performance. Probe delay was manipulated for each species, demonstrating a shift from RI to PI dominance, portrayed by the recency to primacy shift. Closed circles represent accuracy for same trials at each serial position. "Diff" refers to different trials and accuracy is represented by the open triangle.

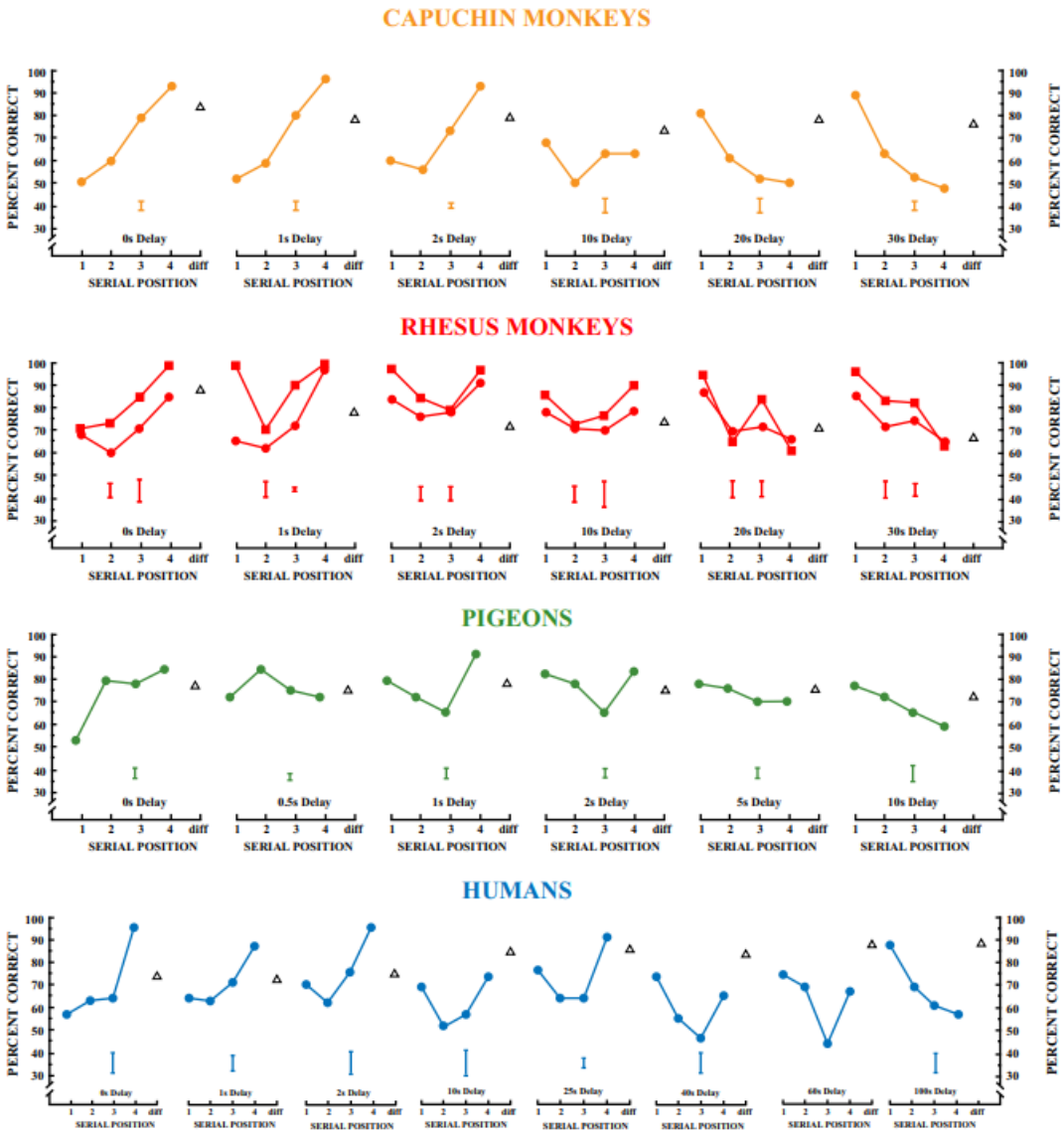


Figure 3.2

From Murdock 1962. As list length increases, there is increasingly worse memory for items occurring earlier in the list. The first number for each number is the list length. The second number is the inter-stimulus interval, which had no effect.

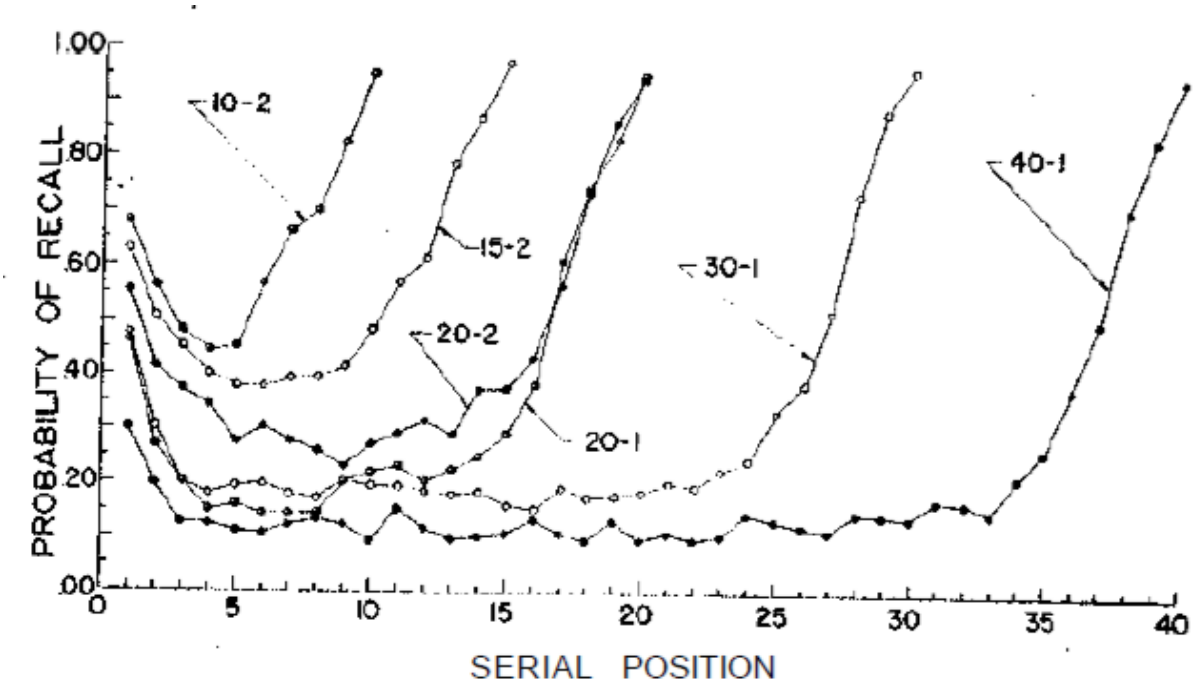


FIG. 1. Serial position curves for the six groups.

Figure 3.3

Schematic of a trial during the dMTS task. Participants start with a ready screen, which ends when they press the spacebar. After that, the sample odor is presented, with instructions to smell the odor and return it to the experimenter. After the sample is the 30-s delay period. After the delay is the test phase, where two odors are presented at once. The participant must select which matches the sample odor and receives feedback depending on whether they are correct or incorrect.

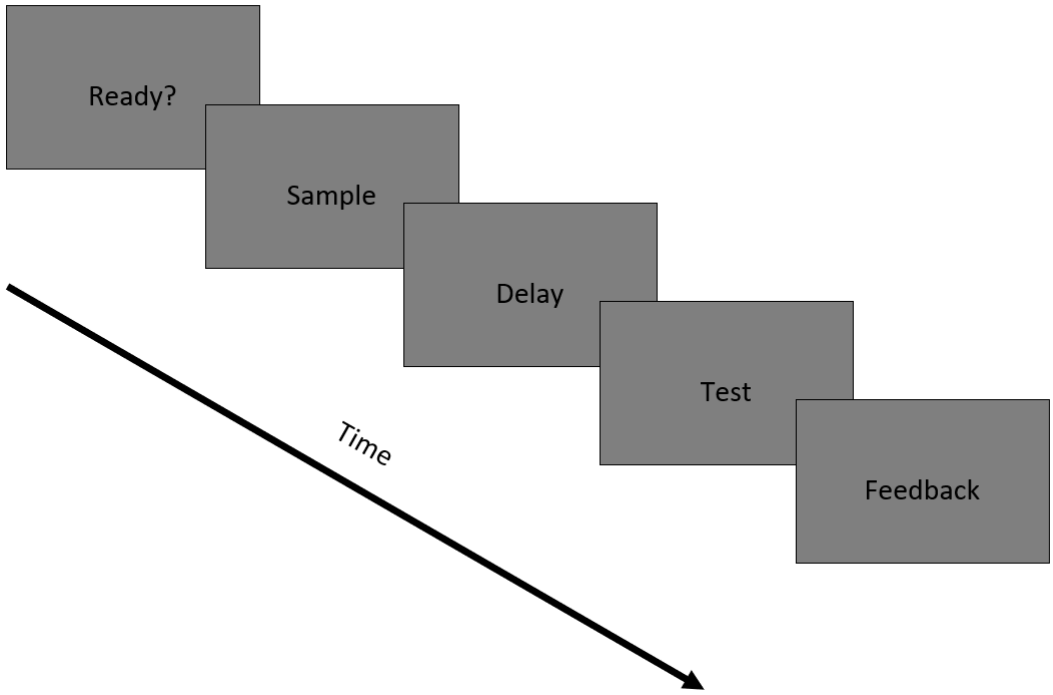


Figure 3.4

Color-coded chart of odor ratings from Experiment 1. Ratings for each odor assigned a color based on relative rating. The highest rating was assigned the darkest green shade, while the lowest assigned the darkest red shade, and yellow represents the 50th percentile rating.

Odor	Intensity	Verb	Pleasantness	Familiarity	Odor	Intensity	Verb	Pleasantness	Familiarity
Allspice	54.31980057	52.11934156	57.60288066	52.80864198	Garlic	89.39643347	67.51028807	44.07064472	75.69615912
Almond	23.60768176	19.97256516	39.92455418	19.71536351	Lemon	76.87928669	57.00274348	56.86899863	58.12757202
Amaretto	62.90466392	40.78875171	52.31824417	39.81481481	Lime	77.1399177	60.28463649	68.19958848	66.60836763
Anise	60.46639232	46.74211248	50.34293553	39.79423868	Maple	29.33813443	26.57064472	44.99314129	31.47462277
Apricot	59.27640604	48.38134431	72.88751715	42.64060357	Marshmallow	46.62894376	39.54389575	57.16735254	36.74211248
Bay	58.54252401	46.41289438	45.84705075	49.28326475	Mustard	23.28875171	13.55967078	25.68587106	19.9382716
Blackberry	72.96639232	65.06858711	81.89643347	66.48491084	Orange	79.6399177	75.20233196	67.08161866	71.61179698
Blueberry	54.26611797	42.13648834	60.49382716	53.87860082	Oregano	64.76680384	41.73182442	36.67009602	38.6659808
Butter	75.35322359	65.02057613	61.13854595	67.39711934	Parsley	45.97736626	39.07407407	39.11865569	33.61111111
Butterscotch	62.47256516	60.67901235	70.47325103	55.82647462	Peach	67.80270655	59.94513032	69.97942387	59.29012346
Caramel	67.12962963	53.65226337	65.62414266	50.43552812	Peanut Butter	73.10013717	58.96433471	73.71399177	63.73575499
Carob	52.37654321	34.74279835	38.28532236	24.62620027	Pecan	69.00548697	41.73525377	50.20919067	45.07201646
Chamomile	66.14197531	46.8861454	51.26200274	49.72565158	Pina Colada	64.61934156	57.75720165	68.05898491	57.76406036
Champagne	71.8484225	46.39917695	54.29355281	42.06104252	Pineapple	49.53017833	35.96021948	62.7297668	48.79286694
Cherry	64.00891632	46.24828532	60.21604938	46.96159122	Raspberry	67.02674897	58.22702332	69.13580247	60.30178326
Cinnamon	88.27503429	63.75514403	53.95747599	57.99382716	Rootbeer	35.86076818	20.79218107	30.22633745	23.42935528
Clove	79.31069959	67.23593964	62.5617284	64.78737997	Rosemary	80.80246914	66.67009602	59.41358025	59.79423868
Coffee	32.80864198	22.88065844	32.88751715	26.12482853	Savory	51.42318244	46.84156379	48.27846365	44.39102564
Coriander	31.10768176	26.08024691	39.49245542	23.77229081	Strawberry	69.8079561	63.35390947	76.5569273	65.29492455
Cotton Candy	58.19272977	49.36899863	51.26780627	40.78532236	Sumac	69.13580247	42.16880342	35.73388203	37.05075446
Eggnog	65.26406036	43.54595336	45.70987654	40.46296296	Tangerine	75.3909465	52.5617284	47.92524005	46.84499314
English Toffee	59.46502058	48.81054131	66.57064472	49.80452675	Thyme	64.75994513	47.16735254	33.51851852	41.61179698
Fennel	55.24005487	31.70438957	32.75377229	27.63717421	Turmeric	64.49245542	26.23799726	27.88751715	27.5308642
Fenugreek	48.60082305	35.37037037	35.29835391	31.08367627	Watermelon	70.54183813	57.03703704	60.72702332	54.72908093

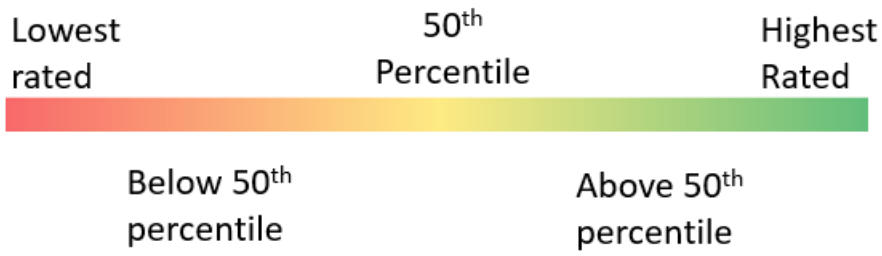


Figure 3.5

Schematic of a trial in Experiment 2. Subjects start each trial with a ready signal. When they indicate readiness, the first odor sample is given to them. After the ISI, another sample is given, and again participants are asked to return the odor to the experimenter. This repeats for the final sample odor. After the list is presented, there is the delay period followed by the probe. Each trial ends with feedback for the participants.

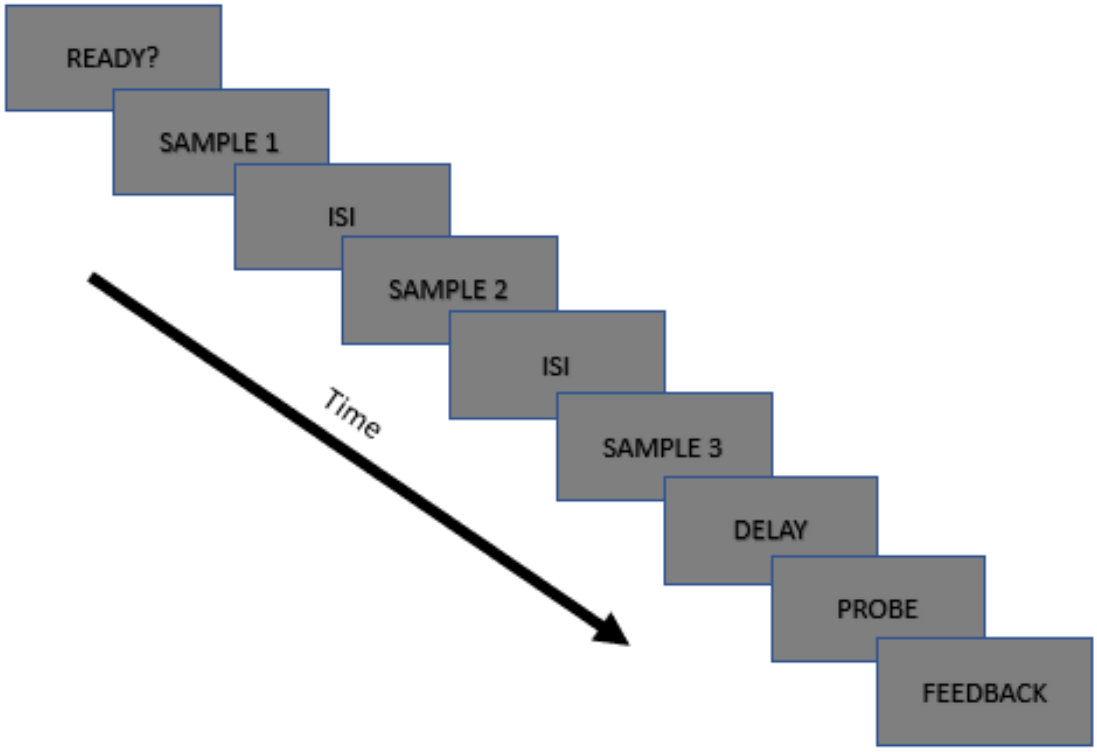
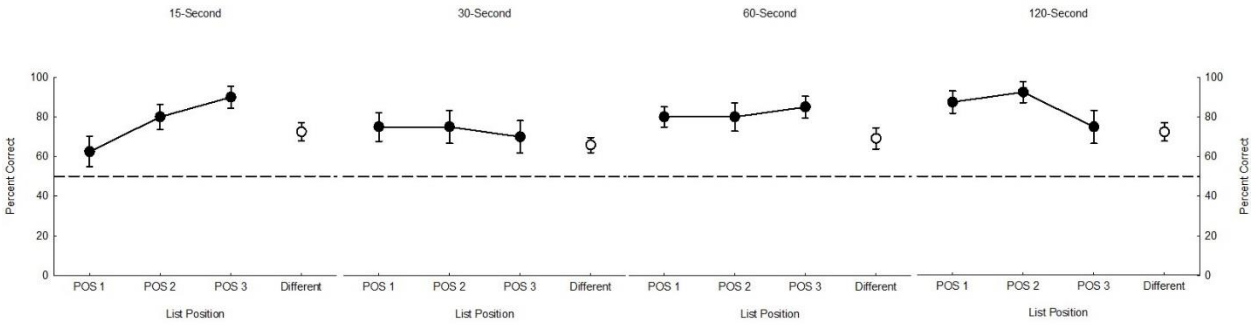


Figure 3.6

Mean data from Experiment 2. Each line represents one SPF at a particular probe delay duration (15. 30, 60, 120 seconds). Filled in circles shows mean accuracy for same trials at that serial position for each delay length, while open circles show accuracy for different trials at each delay length. The SPF for the 15-s condition shows a significant recency effect, while the SPF lines for the 30-s and 60-s conditions are flat. The SPF for the 120-s condition shows a significant increase in percent correct for position one, while the decrease in position three percent is not significant.



Chapter 4: General Conclusions

The study of olfaction lags behind that of other senses. While there is considerable overlap in the way these sensory systems operate, one cannot generalize all findings to all senses. Aside from differences in neuroanatomy, olfaction may have different psychological processes as well. For example, human individuals often find it far more difficult to identify the odor of an apple than to identify the picture of one. Wilson and Stevenson (2003) suggest that a "top-down" approach to olfaction is necessary, as context, expectation, and experience often determine how odor is perceived. As such, the experiments in these chapters explore olfaction in the context of memory.

Chapter 2 outlines two experiments designed to assess the effects of proactive interference (PI) of olfactory stimuli on a matching-to-sample task in dogs. In the first experiment, PI was manipulated by constraining the set of stimuli used to construct each session, referred to as the set size. The set size was either 48, 6, or 2 items. PI through the repetition of stimuli was at its highest at 2 items, while there was no (within session) PI in the 48-item condition. Further analysis found that for dogs, the source of PI comes from the dog's previous choice, rather than perseverating on rewarded choices.

The second experiment from chapter 2 adapts procedures reported by Wright et al. (2012) and Wright and Devkar (2016) to the olfactory MTS task. These previous studies revealed two types of interference, time-based (Wright et al., 2012) and event-based (Devkar & Wright, 2016). Time-based interference functionally depends on the elapsed time between sample and presentation of the test stimulus. When pigeons, for example, experience interference, it is due to the fact that they are indexing memories of the current and past samples using a log transformation of the elapsed time since the current and previous sample were viewed. Monkeys

and, as our results tentatively indicate, dogs experience event-based PI. Confusion as a result of PI comes from the recent events. This could mean that event-based PI is a shared processes amongst mammals.

Chapter 3 shifts focus from dogs to humans. In two experiments, we explore the effects of proactive and retroactive interference on recognition of lists of odors. One of the hallmarks of list learning is that, under certain conditions, memory for the first item in the list and the last item in the list is better than the middle items. Manipulating certain factors, such as the retention interval between list presentation and memory test, can influence the shape of the serial position function (SPF). A short retention interval results in a flat, positive, and linear SPF with a strong recency effect, and a long interval favors the primacy effect, represented by a negative linear SPF. This shift, from recency to primacy with delay, is not always found in olfaction. The results from Experiment 2 were inconclusive, showing recency at a short delay and then a recovery from that effect at the longest delay. However, there was not a complete shift to primacy with delay, as accuracy for both the first item and third item were relatively high. This result does not mean that memory for odors is not subject to proactive interference. In fact, many researchers (Zucco, 2002) believed that proactive interference was so strong that memory for odors was impervious to retroactive interference. This discrepancy likely comes down to differences in methodology. While other studies had explored memory and olfaction, none had systematically varied probe delay in order to determine the point at which recency shifts to primacy.

Future work on olfaction needs to address issues faced in chapter 2 and 3. Namely, methodological differences have produced wildly disparate findings. Some procedures have produced strong proactive interference with no retroactive interference, and yet, in other procedures, there is a strong effect of retroactive interference, as evinced by persistent recency

effects in list memory tasks. Additionally, the role of verbalization in olfaction is not well known.

Overall, the experiments reported in this dissertation advance what is known about olfactory memory in humans and in dogs. This dissertation demonstrates some of the relationships between time, interference, and verbalization can have on olfactory memory. Further, difficulties that were faced can be addressed in future research.

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