Serial-Probe Recognition for Gustatory Objects

by

Thomas Alexander Daniel

A dissertation submitted to the Graduate Faculty of
Auburn University
in partial fulfillment of the
requirements for the Degree of
Doctor of Philosophy

Auburn, Alabama
May 10, 2015

Keywords: taste, gustation, list memory, recognition, working memory

Approved by

Jeffrey S. Katz, Chair, Professor of Psychology
Lewis M. Barker, Professor of Psychology
Jennifer L. Robinson, Assistant Professor of Psychology
Ana Franco-Watkins, Associate Professor of Psychology
Tracy K. Witte, Assistant Professor of Psychology

Abstract

Historically, what we know about human memory was discovered in experiments that used visual or verbal information. As a result, prevailing models of working memory (e.g., Baddeley and Hitch, 1974) rely heavily on visual and auditory components. The current set of studies investigated the possibility of a separate taste-related working memory that functions independently of vision and hearing. Working memory for tastes was tested using a delayed match-to-sample task in Experiment 1. Results show that memories for tastants (i.e., flavorless liquids) can be briefly stored and maintained over a delay, a hallmark of working memory. This representation of a taste-related memory is not dependent on language, as participants successfully completed the task with articulatory suppression present. Two subsequent experiments used a serial-probe recognition task to explore serial-position effects with taste. With lists of three tastants, participants were able to recognize whether a fourth tastant, presented after a delay, was originally present in the previous list. The length of the delay after the taste list predicted accuracy for tastant recognition, with a longer delay creating a primacy effect, and a shorter delay creating a recency effect.

Acknowledgments

This research would not have been possible without the help of several people. First, I'd like to thank Dr. Katz for spending five years of his life to help me become a better student, teacher, and scientist. A deep gratitude goes out to my committee who have been helpful, attentive, and encouraging. Thank you Drs. Barker, Franco-Watkins, Robinson, and Witte for all that you've done for me and this project.

To my wife, friend, and colleague, Maggie: thank you for your help, support, and love. Adam Goodman and Arash Farshid, thank you for letting me distract you with conversations about research, pop culture, and nonsense. John Magnotti, thank you for reinvigorating my love of coffee and whiteboards. To my fellow lab members: I'm sorry that Thach 108E was in a constant state of disarray. That was my fault, and I apologize.

Mom and dad, thank y'all for letting me go off and be a scientist.

Table of Contents

List of Tables

List of Figures

Chapter 1: Introduction

Of the five basic senses, taste is perhaps the least studied and the least understood (Veldhuizen et al., 2011). Even if it has not received the same attention as the other senses, its function is crucial: it portrays information about the qualities and properties of food. Taste can be used to determine what foods are nutritious and what foods are poisonous (Drewnowski, 1997), and a great body of research has been dedicated to taste aversion, or how we learn which things are safe to ingest and which are not (Gaston, 1978; Verendeev & Riley, 2012). The gustatory cortex has even been mapped onto the human brain (Velduizen et al., 2011), and scientists are now beginning to understand how taste information is transferred, on a cellular level, from the tongue to the brain (Chandrashekar, Hoon, Ryba, & Zuker, 2006). However, there has been almost no work done on the subject of how short-term memory interacts with taste. In other words, the ways that the properties of a taste are stored in human memory are still unknown. Is it possible to remember the exact qualities of food? Is it easier to remember the exact taste of the first and last courses of a meal? Or are tastes all remembered equally? Past research on the subject has been mixed (Barker & Weaver, 1983; Vanne, Tuorila, and Laurinen, 1998; Köster, Prescott, & Köster, 2004). The impetus for this study is to better understand how taste memory works, and how it compares to other senses, such as vision or audition, that have received a more thorough empirical investigation.

The goal of this review and subsequent experiments is to establish a framework for studying taste-related memory. The following review will be divided into four distinct sections. First, a brief history of memory research will focus on how psychology began, and continues, to be biased by language-based stimuli. Second, neurological evidence will be presented to establish the existences of independent short-term memory stores for the different senses. Third, a primer on list memory will detail the findings of primacy, recency, and serial-position functions across sensory modalities. Finally, the current literature for taste research will be summarized. Together, these sections will form an argument for why the existence of an independent taste short-term memory store is not only probable, but necessary for a consistent and accurate model of human memory.

Taste memory will be examined across two experiments. Experiment 1 will test the hypothesis that it is possible to recognize a taste over a short delay using a delayed match-to-sample (DMTS) procedure. Experiment 2 will test the hypothesis that it is possible to briefly store a small set (N = 3) of taste-related memories to be recognized after a short delay. By expanding on the procedure of Experiment 1, participants will be required to memorize multiple stimuli, a requirement for most definitions of working memory (Logie, 2011). Using a serial-probe recognition task, it is possible to systematically investigate the presence of capacity and interference for taste memory. Are tastes susceptible to proactive and retroactive interference in a manner similar to vision, audition, or olfaction? Researchers have used serial-probe recognition tasks to demonstrate primacy and recency effects across vision, audition, and olfaction (Wright, 1998; White, 1998), and in so doing, provided evidence that these senses have their own independent short-term stores. The current set of experiments aim to provide evidence of a similar and separate short-term store for taste.

A Selective History of Working Memory

Ebbinghaus (1885/1913) was the first to use empirical methods to study human memory. Using himself as his own subject, he set about to measure how memory changes over time. To do this, he created hundreds of nonsense syllables, all 3 letters in length, following the formula of consonant-vowel-consonant. After trying to memorize a long list of these syllables, he tested his ability to recall these nonsense syllables at different time intervals and measured his own accuracy. He discovered that as time passed, memories were much more difficult to retrieve, and his "forgetting curves" showed that this difficulty occurred not in a linear fashion, but in an exponential one. Immediately after studying the list of syllables, his recall was nearly perfect, but after only just a few minutes, his ability to recall those syllables dropped by nearly 40%. After a delay of 24 hours, he only recalled about 30% of the nonsense syllables studied in the original list.

Ebbinghaus's research started a systematic line of questioning in psychology: How does forgetting occur over time? Why is recall so much better after an immediate delay as opposed to a 24-hour one? What were the limits to memory? To answer this last question, a seminal paper by George Miller (1956) proposed that the ability to remember items is limited by a fixed number. This number, seven plus or minus two, served as an early index of memory's capacity. Memory can actively maintain about seven items in any given situation, according to Miller. Miller came to this conclusion by synthesizing decades of memory research, and because most of this research was inspired by Ebbinghaus, almost all of these studies implemented verbal stimuli and lists. This initial bias in research meant that while the "magic number 7, plus-or-minus 2" appeared to be valid for lists of words, it would not generalize to all facets of memory (Baddeley, 1994).

To explain the results of Ebbinghaus and Miller, Atkinson and Shiffrin (1968) developed the modal model of memory. Under this framework, memory operated on three basic levels: sensory register, short-term store, and long-term store. When the outside world is encountered, it is experienced through the sensory system, and this early information enters the sensory register. There, it is stored for a very brief (< 1-s) time, just long enough to enter short-term memory. Short-term memory is characterized here by its capacity limits and its brief storage duration. Atkinson and Shiffrin (1968) argued, like Miller (1957), that this store could hold 7 ± 2 items, but that this information could only be stored for less than a minute. If this information is actively attended to (e.g., rehearsed), it may then enter the long-term store. Within the long-term store, memories from months or years past may be retrieved. While the modal model of memory supported many of the findings of memory at the time, it was unable to successfully account for how different stimuli changed the outcome of short-term memory. For example, why was it possible to remember 7 digits presented serially, but only 3 or 4 visual, nonverbal symbols? Atkinson and Shiffrin's framework did not provide an immediate solution to this phenomenon, but other researchers soon would.

Baddeley and Hitch (1974) proposed the concept of working memory (WM), a model of memory to describe the active, deliberate, and temporary store of information. This multi-component model of WM argued that memory was not a general process, but rather, it was specialized and compartmentalized based on what types of information were being stored and maintained. This model used three components: the phonological/articulatory loop, the visuo-spatial sketchpad, and the central executive. Accordingly, the phonological loop specializes in auditory and verbal stimuli, the visuo-spatial sketchpad stores visual stimuli, and the central executive acts as a project manager, generally controlling the flow of visual/aural information.

Instead of one general system of memory that processed all external stimuli equivalently, Baddeley and Hitch argued for separate stores for vision and audition. This novel way of conceptualizing memory created new predictions and new hypotheses to test. As researchers began to utilize novel procedures for memory, it became increasingly clear that memory was not just a singular unitary form of storage, and WM replaced most models of short term memory such as the modal model (Crowder, 1982).

Through this three-component model, scientists have been able to explain, describe, and even predict various behavioral phenomena including the phonological-similarity effect, the word-length effect, and interference between visual and spatial tasks (Baddeley, 2003). This modular approach to WM works well with many of the commonly studied stimuli in cognitive psychology: words, lists, and digits. This model, however, is not as well suited for stimuli presented outside of auditory, visual, or language-based domains. Humans experience external stimuli beyond visual, aural, or verbal information, Is there no touch WM? Olfactory WM? Taste WM? Baddeley and Hitch's model supposes two short-term stores for visual and auditory stimuli, so how does that account for information from other sensory modalities that appears to be temporarily stored and manipulated across a delay? As of the time of writing, there is no consistent or satisfying answer for these questions. Currently, the multicomponent model provides answers for other modalities by representing these stimuli with other representational codes, such as language. For example, one can code a taste stimulus as "salty" or "minty", or code a touch stimulus in terms of visual or spatial representations (Gilson & Baddeley, 1969). The question remains then, how are these representational codes created, and how are they transferred from one store to another?

Perhaps not surprisingly, the multicomponent model of WM has not been without its share of criticism. Chief among these criticisms is the model's inability to explain memory for non-visual, non-aural information. Baddeley and Hitch (1974) did not include a component for touch information, for example. If the structure of memory included components for visual and aural stimuli, how are humans able to remember the location and texture of tactile objects on the skin (Giles & Baddeley, 1969)? In order to address these concerns, Baddeley proposed a new

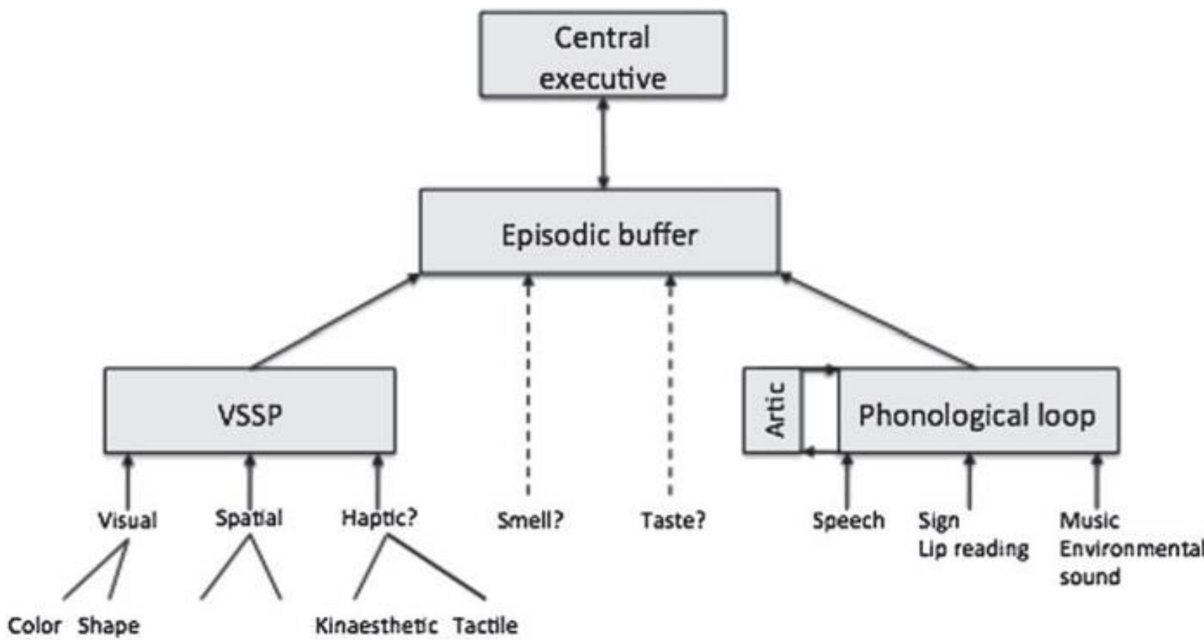

Figure 1. Figure from Baddeley (2012) showing a visual representation of the WM construct. While visual and auditory/verbal information is modularized within their own stores, there is no conclusive prediction for smell, touch, or taste.

component for WM: the episodic buffer (see Figure 1). The inclusion of this additional module allows stores that were previously independent from one another the ability to communicate and share information. Accordingly, the episodic buffer is capable of storing and manipulating multi-dimensional information by translating it into an interpretable code. For example, sensations of touch can be translated into a visual code, where it is then handled by the visuospatial sketchpad.

However, with the exception of a few notable studies (Goldman-Rakic, Cools, & Srivastava, 1996), neurological evidence supporting the existence of the episodic buffer and its interaction with independent memory stores has been difficult to produce.

Neurological Evidence for Independent Short-Term Stores

Increasingly, neurological evidence supports a framework of memory that is based on individual sensory stores, where each store maintains its own version of short-term memory (Postle, 2006). Under this framework, there are hypothesized visual, auditory, tactile, olfactory, and gustatory short-term memory stores that can independently function without creating interference with one another. For example, one may be able to briefly store auditory and visual information without any loss to the original representations of each, but if additional visual or auditory information is encoded, the original representation experiences some quality loss. Thus, the memory of an abstract painting is not disrupted by hearing or repeating verbal materials. These mechanisms help clarify one of Baddeley's (1992) explanations for how articulatory suppression decreases memory for verbal items but not nonverbal items; the auditory representation of words, entering the phonological loop, interferes with whatever information is already temporarily stored in the phonological loop. However, some of the most compelling evidence for this theory arrives via the discovery and investigation of agnosias.

Evidence from Neurological Impairment. Loosely defined, agnosias are neurological disorders that are marked by a patient's inability to consciously recognize an event, but their nervous system is able to actively perceive it. For example, visual agnosia is characterized by a patient that verbally reports being blind, but his or her eyes are still functional, allowing the patient to engage and interact with the environment as if they indeed had sight (Farah, 2004). Accordingly, a patient may have the ability to describe all of the visual properties of an object, but have no recollection of it nor the ability to put the object into words. This phenomenon is completely modular and specific to vision, so memory for any other form of information is kept completely intact. Similarly, prosopagnosia – or the specific inability to recognize faces – suggests that visual information may further modularized into subcategories (McNeil & Warrington, 1993; Farah, Wilson, Drain, Tanaka, 1995). This disorder highlights the existence of independent sensory stores because lesions to specific areas result in the loss of recognition for a very specific type of information. The existence of such agnosias, suggest that not only is the traditional multicomponent model of working memory incorrect, but that a dramatically new model of memory is needed to successfully describe how memory works.

Auditory agnosias have also been discovered in patients suffering from damage to the temporal lobe, where perception for audition occurs (Clarke, Bellmann, Meuli, Assal, & Steck, 2000). Under these circumstances, patients may react to auditory stimulation, but deny recognizing, or even hearing, the stimulation in question. Support for modality-independent sensory stores can be derived from the existence of nonverbal auditory agnosia (Saygin, Leech, Dick, 2010), where patients maintain all verbal language skills, but are unable to perceive nonverbal, nonlingual sounds. For these patients, a lesion to Wernicke's area leaves the ability to language intact, but sounds, such as noises from animals, the environment, or machinery, can no longer be recognized. Patients exhibiting either form of auditory agnosia are able to demonstrate normal memory for other senses and modalities, but only their memory for auditory items is disrupted. This strongly suggests that auditory memory is housed in a localized portion of the brain and that it functions independently from other modalities. However, if a phonological loop should exist, as Baddeley argues, the distinction of memory between verbal and nonverbal sounds would be impossible. The Baddeley model would predict that one auditory store exists, and that, if damaged, sounds could not be stored within WM, regardless of its specific properties (i.e., verbal, nonverbal).

Considering visual and auditory agnosia, it may still be possible to argue for the multicomponent model of WM because these two senses fit squarely within the framework of the visuospatial sketchpad and phonological loop, respectively. The discovery of an agnosia outside of the conventional senses of vision and audition would support a modality-independent framework of memory. Currently, agnosias have been discovered for touch (Reed, Caselli, & Farah, 1996; Platz, 1996) and olfaction (Mendez & Ghajarnia, 2001). When areas of the brain commonly associated with these senses (i.e., the somatosensory cortex, olfactory cortex) are damaged, patients may retain their ability to use those senses, but their ability to recognize or remember anything derived from those senses completely absent. Evidence for gustatory agnosia is less prevalent, but studies suggest that lesions or ablations to the gustatory neocortex may result in a complete inability to recognize tastes (Kiefer, Leach, & Braun, 1984; Kiefer & Orr, 1992; Small, Bernasconi, Bernasconi, Sziklas, & Jones-Gotman, 2005). Further evidence is needed to parse the contributing effects of agnosias and neurological impairments on memory, as the distinction between perception and recognition becomes blurred in these contexts.

Evidence from Neuroimaging Techniques. With the advancement of neuroimaging techniques like functional Magnetic Resonance Imaging (fMRI), researchers now have the ability to measure the brain activity and neural networks that underlie memory. It is now possible to test whether a construct like Baddeley and Hitch's (1974) multicomponent model of WM exists on a biological level. Two meta-analyses compared the neural activation of participants across scores of WM studies and found distinct networks for verbal and nonverbal memory (Owen, McMillan, Laird, & Bullmore, 2005; Rottschy et al., 2012). When participants are required to remember information that can be verbalized, such as words, letters, or numbers, activation in areas related to language (e.g., Broca's area, lingual gyrus) increased. But when required to remember information that was difficult to verbalize, such as faces or abstract patterns, activation in the premotor cortex increased instead. These findings are not contrary to the multicomponent model of WM, and in fact, they support the idea that visual and auditory/verbal information is retained in their own distinct, separate short-term memory stores. When applying these same methods to non-visual or non-auditory stimuli, however, significant deviations from the multicomponent model of WM arise.

Using fMRI, Zelano, Montag, Khan, and Sobel (2009) used a serial-probe recognition task with varying delay lengths to examine the interaction between olfaction, memory, and verbal coding. Of primary interest to the researchers was 1) whether memory for odorants demonstrated different areas of activation based on how easily those odorants could be verbally labeled, and 2) what role verbal labelling played with varying delay lengths Odorants were presented while participants were being scanned in an MRI bore; the first stimulus was presented, and after an average delay of 5 to 10 seconds, the second stimulus was subsequently presented. Responses were made based on whether the second stimulus was the "same as" or "different than" the first stimulus (a simple N -1 task). Odorants were classified as either nameable or nonnameable based on participants' ratings in another task before entering the scanner.

The authors found a difference in activity between nameable and nonnameable stimuli; when odorants were nameable, areas associated with language, such as the opercular, orbital, triangular inferior frontal gyrus, and Broca's area, showed sustained activation over the course of the delay period. However, when odorants were nonnameable, activation shifted to areas in the primary olfactory cortex. In other words, when participants specifically remembered the smell of an odorant rather than its name, the primary olfactory cortex showed higher levels of activation than areas associated with language. Based on these differences in network activation, it may be inferred that the representation of the memory was stored as an odorant rather than as a verbal label. Because participants identified verbal labels (or not) on an individual basis, these differences in activation were individualized to each participant and sensitive to individual reports. In this way, the researchers could confirm that there was nothing particularly special about the odorant itself, but rather, localized activation was dependent on how participants individually characterized these stimuli. These findings confirm Postle (2006) and Wickens' (1991) claims that the brain recruits the most efficient representational code for memory. Because some of these odorants could have verbal/lingual codes, these memories were better handled by the lingual regions of the brain in the temporal lobe.

Harris, Miniussi, Harris, and Diamond (2002) found that tactile memory manifests as localized effects similar to those of vision and olfaction. Across two experiments, memory for vibrotactile stimulation was measured across different retention intervals with and without transcranial magnetic stimulation (TMS). The first experiment tested memory for vibrotactile stimulation when applied to the index finger, and then compared to the index finger of the same hand or the opposite hand. For the second experiment, TMS allowed researchers to disrupt memory for tactile stimuli by temporarily disabling the primary somatosensory cortex. Participants experienced a vibration on their index finger, after which a 1500-s delay was presented. By the end of the delay, a second vibration was presented to the index finger, and participants were asked to judge the second presentation as faster or slower than the first presentation. According to the revised model of WM as proposed by Baddeley (2000), the episodic buffer should be responsible for interpreting the tactile stimuli as it relates to the central executive. The results of the first experiment show that across retention intervals of 300, 600, 900, and 1200-ms, there is no a significant decrement in memory when the sample and probe vibration were presented on the same finger. However, when the stimulation was presented across left or right index fingers, accuracy on the task was significantly lower but only during 300 and 600-ms delays. At 900-ms and greater, there was no difference in recognition. All results of the second experiment were compared to how participants performed when experiencing TMS in an adjacent area (as a control condition). If TMS occurred within the first 600 ms of the stimulus presentation, participants could not reliably compare the two rates of vibration. However, there was no difference if TMS occurred at 900ms or higher – participants could recognize the vibrations just as well as in the control condition.

What the data collected by Harris et al. (2002) suggests is that memory for tactile objects has a brief short-term store similar to that found in vision and olfaction. As soon as a tactile stimulus is experienced (like the vibrotactile stimuli applied to the index finger), the primary somatosensory cortex temporarily stores this information before it is later integrated into the rest of the sensory system. These results are similar to Pashler's (1988) findings with vision: within a short timeframe, accuracy is nearly perfect, but after a longer delay, performance steadily decreases. When a mask is applied, such as a white-and-black checkboard screen in a change detection task, the recognition accuracy significantly drops. For Harris et al., TMS served as a mask for tactile stimulation, and performance decreased accordingly. However, at the longer retention intervals, the memory for vibration was no longer housed solely in the short-term store of the primary somatosensory cortex, so TMS did not disrupt memory for these vibrations. These findings are not currently accounted for by the multicomponent model of WM (Hurlstone, Hitch, & Baddeley, 2014), and they provide further evidence towards the fractionation of sensory modalities in short-term memory.

List Memory, Primacy, and Recency

Given a list of words, people are very good at remembering the first and last few words of the list. This effect was noted during Ebbinghaus's (1913) early investigations, and he was the first to coin the phenomenon the "serial position effect" (see Figure 2). The serial position effect is composed of two components: primacy and recency. The primacy effect describes the high levels of accuracy for words presented early in a list, and the recency effect describes the high level of accuracy for words presented at the end of a list. The most common way to study these effects is the list memory procedure, where participants observe a list of words, are introduced to a delay, and then asked to recall the list of words in full.

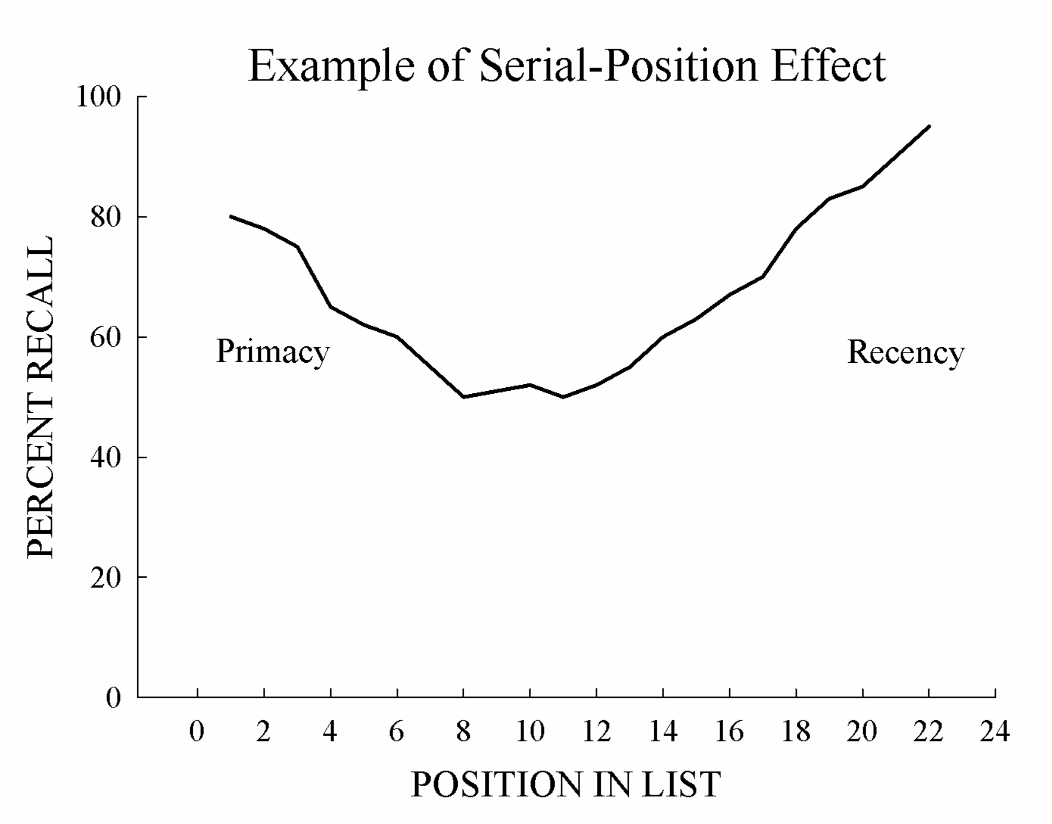

Figure 2. A theoretical serial-position effect. Recall is highest during items at the beginning (primacy) and ending (recency) of the list. Accuracy is poorest for items presented in the middle of the list.

However, it is not always practical, or possible, to recall a list in experimental settings. Extending from Ebbinghaus's research, this procedure has been adapted into a recognition procedure (Deese & Kaufman, 1957; Murdoch, 1962), so that participants respond on the basis of whether the probe stimulus was previously present in a list of stimuli or if it was different from each stimulus in the current trial's list. A typical serial-probe recognition task operates thusly: stimuli are presented in serial order, a delay separates the list and the probe stimulus, and when the probe stimulus is presented, participants respond whether or not they recognize the stimulus from the current trial's list. Such a task allows researchers to investigate memory for stimuli other than verbal words or verbalizable pictures because participants are no longer required to recall a response. After all, it would be difficult or impossible to verbally identify or name stimuli such as sine-wave patterns, abstract polygons, vibrotactile stimuli, or unfamiliar tastes, for example. With this serial-probe recognition task, Weaver and Stanny (1978) used pictorial, nonverbal stimuli to establish the serial-position effect, an effect that was replicated with nonhumans just a few years later (Sands & Wright, 1980).

Wright, Santiago, Sands, Kendrick, & Cook (1985), using nonverbal visual items in a serial-probe recognition task, demonstrated serial-position curves for humans, pigeons, and rhesus monkeys. See Figure 3 for serial-position curves across species and retention intervals. These data suggest two important theoretical implications: a) primacy and recency are sensitive to task-specific parameters such as probe delay length, and b) these effects are the direct result of memory interference. For all species, when the probe delay length was short (e.g., 0 – 2 s), retroactive interference disrupted the recognition of items presented early in the list, and accuracy was at its highest for the items presented last (i.e., recency). When the probe delay was longer (e.g., 100 s), proactive interference disrupted the recognition of items presented at the end of the list, and accuracy was highest for items presented first (i.e., primacy). However, the serial-position function was recreated when using intermediate delay lengths (10 – 40 s) in humans, suggesting that the U-shaped function is a combination of proactive and retroactive interference, increasing the recognition for the first and last items in the list. Importantly, these functions were obtained using a set of kaleidoscopic images, and these images are colorful, visually complex, and nonverbal in nature. Later research investigated the impact of verbalizability on the serial position function.

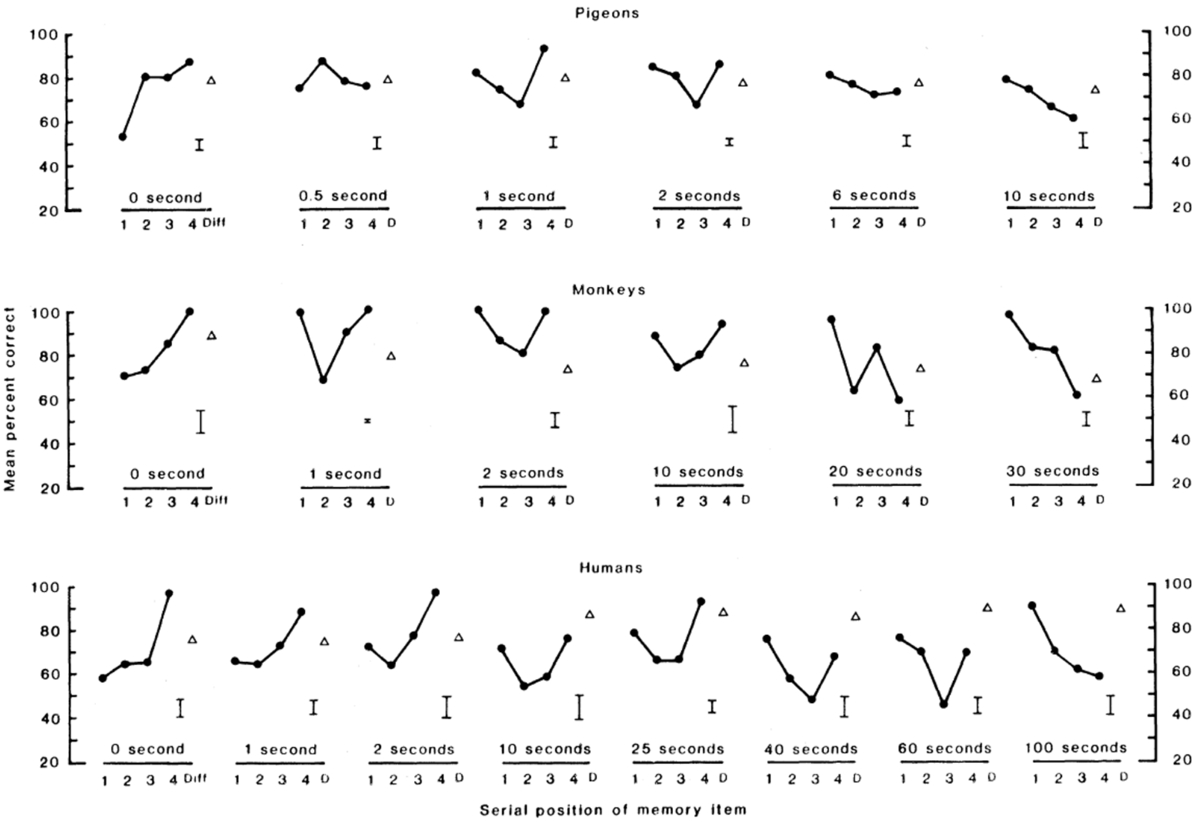

Figure 3. Figure originally appeared in Wright et al. (1985). Serial-position effects are shown for three species (pigeons, monkeys, and humans) across a variety of probe delays. For these lists, a 0-s delay resulted in a recency effect, and the longest delays resulted in a primacy effect. These effect are a function of probe delay, with proactive and retroactive interference differentially affecting recognition accuracy.

Wright, Cook, Rivera, Shyan, Neiworth, & Jitsumori (1990) had participants apply verbal labels (e.g., names, words) to 32 kaleidoscopic discs before performing in a list memory task. After the study, individual participants were asked about the strategies they used to solve the list memory task. While all strategies demonstrated the U-shaped function of primacy and recency, the strategies participants used impacted their ability to recognize the kaleidoscopes. Participants that reported using verbal labels to describe the traditionally nonverbal stimuli demonstrated the highest accuracy on the list memory task. Conversely, the participants that reported employing sensory-based strategies not involving verbal labels demonstrated the poorest accuracy in the task. These findings stress the importance of verbalizability in memory tasks: although the same stimuli were used for all participants, those that performed the task as if it were composed of words performed best, whereas those that focused purely on perceptual qualities of the stimulus, such as the fractal pattern, performed worst. If memory is being studied for visual, auditory, or any other sensory stimuli, ruling out verbalization is important in order to draw any meaningful conclusion about that process of memory.

To date, list memory procedures have been employed for visual, auditory, olfactory, and tactile lists. Serial-position functions have been established for visual and auditory stimuli, and each modality responds differently to the manipulation of parameters such as delay length and interstimulus interval (Wright, 1998). List memory with touch and odorants has, however, produced less clear results. Watkins and Watkins (1974) and Manning (1978) first provided evidence that tactile sensory memory were independent from other senses, but it was not until Nairne and McNabb (1985) adapted tactile sensations into a list memory task that serial-position was studied. The researchers produced primacy and recency effects by using a serial-recall task wherein participants learned a 9-item sequence of finger presses. While accuracy in the task was highest on the first and last few items in the list, it is impossible to discern whether or not these finger presses were represented as lingual, or even motor, codes. According to a comprehensive review of tactile memory by Gallace and Spence (2008), this has been the only list memory task attempted, and further investigation is warranted to draw any meaningful conclusions about serial-position effects in touch.

Similarly, research in olfaction has produced unclear evidence for serial-position effects. Neither, White and Treisman (1997) nor Miles and Johnson (2005; 2009) found strong evidence to support a full serial-position effect when using lists of odor-based stimuli. Accuracy was highest for the last items in the list, suggesting a recency effect, but neither group found evidence for primacy. Two explanations may explain the lack of primacy: a) odor memory may be qualitatively different from visual, auditory, and tactile memory because it does not allow for primacy, or b) neither of these research groups systematically manipulated some of the key task-parameters of the list memory task. Wright (1998) offers an account of how proactive and retroactive interference can differentially effect primacy and recency for visual and auditory items, and these effects are reliant on delay length, intertrial interval, interstimulus interval, and set-size. For vision, increasing the probe delay length results in a shift from a strong recency effect to a strong primacy effect, with the intermediate lengths created a traditional serial-position function. But for audition, the probe delay carries the exact opposite effect, and short delay lengths result in strong primacy effects, long delay lengths in strong recency effects. With this knowledge, olfaction may not obey the same rules that vision or audition does in regard to delay length, or any other task parameter. Because none of these parameters were directly manipulated regarding olfaction, it is impossible to completely rule out a primacy effect. According to these authors, odors may not represented in the same manner as visual or auditory information, and instead, the label (i.e., the word that is used to verbalize the odor) is often remembered in its place.

Using a list memory task, Johnson and Miles (2009) explored how participants' perform across varying sensory modalities. Across a 6-item serial list, unfamiliar faces were used for nonverbal visual items, pure tones were used for auditory items, and 50 different smells were used for olfactory items. Lists used only within-class stimuli, so that only olfaction was needed, or vision, or audition. Participants were presented each item for 1 second, and after the final list item, a 3 second retention interval was used before recall. A probe was presented, and participants had to recall what position on the list (1-6) that item was presented on. In almost every respect (except stimulus presentation), the parameters and methodology were held constant for each modality's lists. Maintaining the criterion for WM, participants would need to temporarily store this information for later comparison and recall.

The three stimulus modalities presented show different serial-position functions, showing that performance was different depending on whether or not the stimuli were visual, auditory or olfactory (cf. Figure 3, Johnson & Miles, 2009). These curves were qualitatively different as well, suggesting that these stimuli were not encoded, maintained, and stored in the same way.

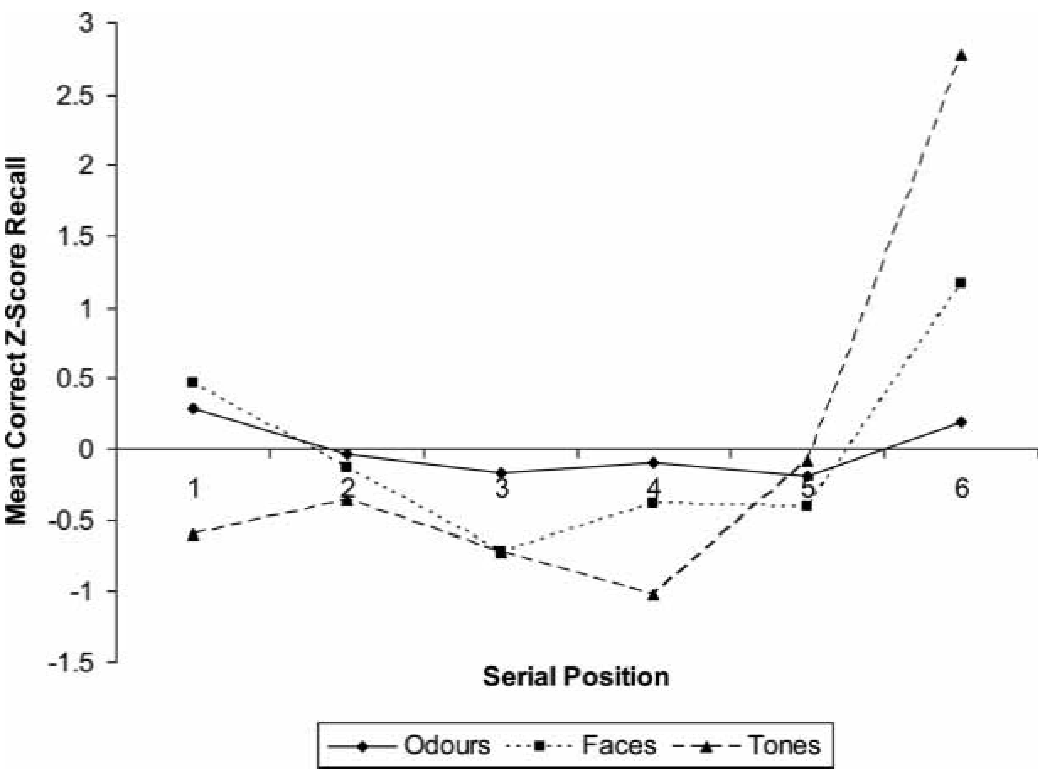

Figure 4. Figure from Johnson and Miles (2009). By standardizing position-recall accuracy, recency effects were found for nonverbal auditory (dotted line) and nonverbal visual stimuli (dashed line). Accuracy for olfactory stimuli (solid line) did not differentially change across list position.

These behavioral results offer evidence for a more modular view of WM – they only truly contradict the multicomponent model in the sense that there is no "olfactory store" available to account for these effects. Andrade and Donaldson (2007) found similar results and also suggested that their effects were due to a modality-specific model of WM. Other studies that have shown olfactory memory to not be dissimilar from vision and audition (Ward, Avons, & Melling, 2005), but these studies use small stimulus-sets (increasing the likelihood of proactive interference) and verbalizable stimuli. Because Johnson and Miles (2009) uses 50 separate odorants, it is unlikely that participants are able to apply verbal labels to each of these stimuli or suffer too seriously from proactive interference. Converging evidence would be needed to answer the question of whether or not there exists the same odorant-independent network in memory like in VSTM. But taken together with the findings of Zelano et al. (2009), these data support an odor short-term store that is independent from other senses.

Taste: Perception and Memory

Sensation and Perception of Taste. Of the remaining four basic senses, taste interacts the most with olfaction (Murphy & Cain, 1980). These two senses are the only senses that use chemoreceptors, meaning that the sensation created by odor and taste are the result of chemical changes in the nose or tongue respectively. The overlap between these senses have created confusion about where perception for one sense begins and the other ends. For example, Rozin (1982) notes that the general public views "taste" and "flavor" as interchangeable terms. However, flavor is the perception that results from the combination of olfaction and taste together. While other factors may affect the perception or quality of flavor (e.g., temperature or texture), flavor cannot be perceived without either taste or olfaction: removing one of these senses eliminates the percept entirely. To make matters more confusing, the presence (or manipulation) of one of these senses influences how the other is perceived. To put another way, altering the odor properties of an item changes the way the taste is perceived (Stevenson, Prescott, & Boakes, 1999) and vice versa (Green, Nachtigal, Hammond, and Lim, 2012). This interaction with olfaction is similar to that found between vision and audition (Spence, 2011), so although these two senses are highly related, it may be assumed that they have independent short-term sensory stores as well.

Taste also differs from other senses in that it is composed of five basic individual sensations: saltiness, sourness, sweetness, bitterness, and umami (Chandrashekar, Hoon, Ryba, & Zuker, 2006). These sensations are derived from chemical reactions that take place mostly on the tongue. Salty solutions contain sodium ions, and the perception of saltiness results from the detection of these sodium ions. Sourness results from a solution that contains acidic elements, and its perceived taste is the detection of this acidity. Sweet solutions are normally derived from aldehydes and ketones, associated with saccharine and sucrose, and the perceived taste of sweetness is the activation of G-protein-coupled-receptors (i.e., T1R1, T1R2, and T1R3). Bitter solutions defined by their often salient and aversive ingredients, including coffee, quinine, olives, or cocoa, and the perceived taste of bitterness is the result of receptors activated by gustducin, a G protein. Umami, (also known as savory) is the most recently discovered taste (Li, Staszewski, Xu, Durik, Zoller, & Adler, 2002), being formally canonized with the discovery of unique taste receptors that activate only in the presence of specific forms of glutamate (Chaudhari, Landin, & Roper, 2000). There is still much controversy over new potential basic tastes (Chandrashekar et al., 2009), and the current list of 5 basic tastes may expand with the inclusion of hotness and/or carbonation.

The limited amount of basic tastes available to human perception provides an inherent limitation on how many tastants can be remembered or recognized. Where vision and audition can use a nearly infinite combination of shapes or sounds, taste is limited to the 5 basic tastes and the solutions they may create when mixed. Bartoshuk (1978) and Köster, Presecott, and Köster (2004) found that the just-noticeable-difference (JND) for tastants varies greatly based on the basic tastes beings measured. For example, in an incidental memory task, for participants to notice a difference between tastes, solutions need to be nearly doubled in concentration. This increased concentration ranges from 1 g/l (for bitter caffeine) to 13 g/l for (for sugar in orange juice). Breslin and Spector (2008) detail evidence for less varied JNDs, but warn that multiple factors can influence a participant's perception of taste intensity, such as where the tastant is administered on the tongue, the quality of the compound being tasted, genetic predispositions, and pre-existing tastes in the mouth. Accordingly, JNDs for taste have been difficult to measure reliably across experiments, and generalization of one study's findings should be approached with caution.

Another significant limitation of taste research is the ability to present pure tastants and pure controls. Consider a visual memory task, where participants are require to memorize a list of abstract polygons. During the retention interval, a blank screen is often shown so that no competing visual cues interrupt the currently stored information. To our knowledge, there is not analogous blank screen to separate individual tastes. For example, in Bartoshuk's (1978) examination of absolute thresholds in taste, distilled water was perceived differently based on the previous taste solution administered. While distilled water carries no chemical properties that would naturally create a taste percept on its own, participants report that it tastes "bitter-sour" after following a salt-based solution. After acidic or bitter substances, it may taste "sweet". Such perceptual confusion varies widely, with factors such as genetic predisposition and how much saliva is currently present in the participants' mouths exacerbated or attenuating these effects. Distilled water is currently used as a palette cleanser to separate individual tastants, but its potential compensatory effects must be considered in taste studies (Johnson & Vickers, 2004).

Current Research in Taste Memory. Within the domain of memory, taste research has been sparse, and nearly all approaches to the subject do so within associative learning frameworks and do not address short-term memory (Núñez-Jaramillo, Ramírez-Lugo, Herrera-Morales, & Miranda, 2010). Barker (1982) argues that taste memory may be vastly different from visual/verbal memory for a few key reasons: 1) humans are born predisposed towards certain tastes over others, 2) these predispositions change throughout the human lifespan, and 3) modal-specific factors make tastants experienced differently than images/words (i.e., intrinsic flavor quality, duration of contact with the tongue, post-ingestion consequences, and flavor "rehearsal"). The few tests that have investigated taste short-term memory have produced strange, counterintuitive results. For example, Barker and Weaver (1983) demonstrated that memories about taste are subject to immediate and permanent interference, and judgments about absolute intensities of a taste may be impossible. In their study, participants were given one of two dilutions of sucrose (sweet) solution, one of four delays ranging from 1 m to 72 hrs, and then asked to recall the intensity of the original solution compared to a new solution. Even at the shortest delay, participants reliably reported the original solution to be weaker than the new solution when the two had the same sucrose content. In other words, when tested with the same sucrose concentration, participants rated the new solutions as being sweeter. Barker and Weaver (1983) argue that these data are evidence that taste *cannot* be accurately represented in memory, and that memories for specific tastes are subject to rapid interference. These findings were replicated by Köster, Prescott, & Köster (2004) using an incidental learning procedure with a delay of 8 hrs, but other researchers have found slightly different results.

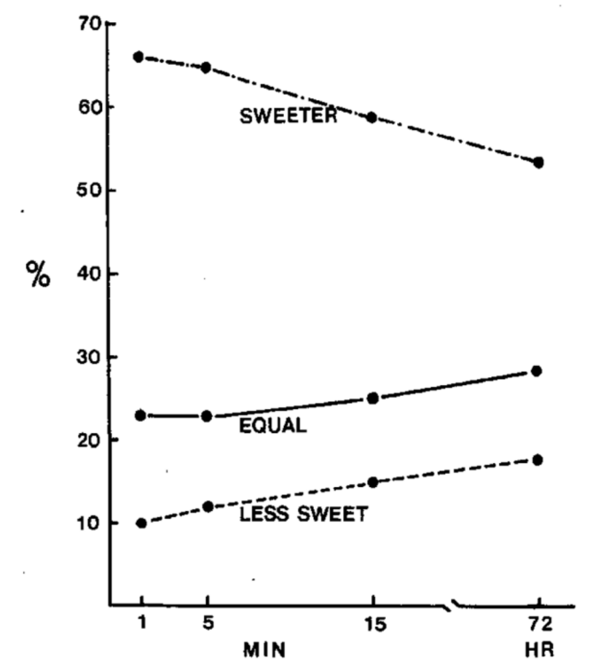

Figure 5. Figure from Barker and Weaver (1983). Participants were far more likely to report that the probe tastant was sweeter than the sample tastant. This effect was most dramatic after a 1-m retention interval.

Vanne, Tuorila, and Laurinen (1998) replicated Barker and Weaver's (1983) effects using a similar task. Dilutions of sucrose were mixed with either water (as a control) or a dilution of either sodium chloride (salty), citric acid (sour), or caffeine (bitter). After varying delays, participants were asked to recreate the sweetness intensity of the sample liquid. Participants reliably miscalculated the absolute intensity of sweetness, but unlike Barker and Weaver's (1983) findings, the testing solutions were generally sweeter than the sample. In other words, when participants were able to recreate their memory of sweetness intensity, they reliably created solutions that were more intense than the original tastant. Additionally, the researchers found that additional, irrelevant tastants (i.e., sodium chloride, citric acid, or caffeine) had no effect on how participants remembered the sweetness intensity. This finding runs contrary to Stevenson and Prescott's (1997) finding that combining tastes reduces the remembered intensity of both tastants. The differences of Vanne, Tuorila, and Laurinen's data and that of Stevenson and Prescott's and Barker and Weaver's is likely due to task-specific details, such as having participants mix their own solutions *ad libitum* (Köster, Prescott, & Köster, 2004). Further commentary by Morin-Audebrand et al. (2012) posits that taste memory's function is to detect changes in tastes rather than recognizing previous encountered food.

Other studies have tried to investigate taste short-term memory, but failed to control contributing effects for olfaction. For example, Melcher and Schooler (1996) report how experts and novices of wine-tasting differentially remember the taste of a wine. After a short delay (4 m) and distractor task (verbal or nonverbal), participants considered experts were much better at remembering the original wine sampled than novice or intermediate wine consumers. For these experts, neither the verbal or nonverbal distractor task had an influence on their ability to remember the original wine. However, because this study did not control for flavor or odor, these data are less relevant to taste memory as they are to expertise, as there is no way to be sure if the experts were using taste, odor, olfaction, or a verbal label to recognize the wine. Parr, Heatherbell, & White (2002) would later show that wine experts have a better ability to recognize odors than absolute intensities of tastes. A similar study to Melcher and Schooler was conducted by Valentin, Chollet, Beal, and Patris (2007) with varying levels of expertise with beer. Beer experts were able to better memorize tastes during the recognition task, but only whenever they had prior experience with that particular beer. This suggests that the advantage that experts had in recognizing beer was less driven by taste short-term memory or perceptual sensitivity than it was by long-term memory and past history with the taste. Taken together, these studies stress the importance of verbal labels, and when a participant has the ability to verbally code a tastant, that tastant will be easier to recognize in the future (also see Engen & Ross, 1973)

Reed, Croft, and Yeomans (1996) may have provided the first test of serial-position functions in taste-related stimuli. This study, however, was not interested in taste memory, but instead, in non-spatial memory for rats. Because memory in rats is often studied with visual or spatial cues, Reed et al. created a task that could only be solved with the use of non-spatial, non-visual cues such as olfaction or taste. Rats were presented with an array of 5 liquids, presented serially. These 5 liquids were commercially-available food flavorings: banana, brandy, lemon, orange, and sherry. Rather than measuring a binary “same” or “different” recognition response, the experimenters recorded the amount of probe liquids that were consumed, thus relying on rats’ natural avoidance of novel flavors (i.e., neophobia). After a delay of 0 s or 30 min, rats showed a propensity to return to the liquid presented either first or last in the array, creating the U-shaped function of the serial-position function. This finding shows that rats have some ability to remember non-spatial, non-visual cues, but which ones? Rats had access to the stimuli’s odors, tastes, and flavors, so it is impossible to discern which cue, or which combination of cues, were used to discriminate these liquids.

A recent attempt to test for recognition-memory in gustatory stimuli found some evidence for a primacy effect (Johnson, Volp, & Miles, 2014). Using 3-item lists, participants were presented with lists of tastes or non-verbal visual stimuli. For both modalities, the same 4 stimuli were used throughout the study; taste lists were always the same 4 wines (two whites, two reds), and visual lists were always the same 4 black-and-white patterns. Participants were able to taste each wine for 5 s followed by a 5-s interstimulus interval. The delay between the 3-item list and the recognition probe was also 5 s. On trials where the recognition probe was not presented in the 3-item list, a novel taste or matrix was used as a distractor. Participants were able to reliably recognize whether probes were presented in the previous 3-item list, and this recognition varied based on the list position. However, these serial-position functions differed based on the modality used with tastes showing a primacy effect, and black-and-white patterns showing a recency effect. Johnson et al. use these data to argue for qualitative differences in memory processing for gustatory and nonverbal visual information, but this assertion requires qualification.

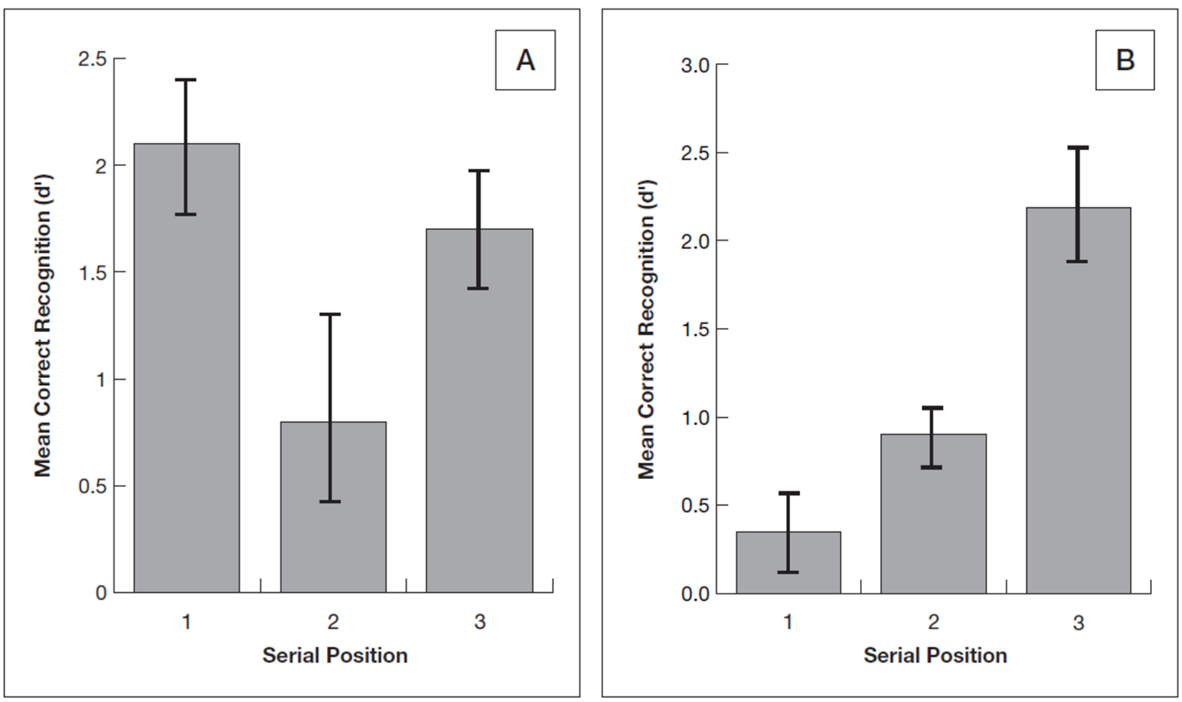

Figure 6. Figure from Johnson, Volp, and Miles (2014). Mean sensitivity (d') was calculated for each list position for wines (Panel A) and black-and-white patterns (Panel B). For wines, a primacy effect was found (all other positions not different from chance), and for black-and-white patterns, a recency effect was found (other positions not different from chance).

In demonstrating recognition-memory for gustatory stimuli, Johnson et al. (2014) were unable to successfully rule out the possibility that participants were using verbal coding. While verbal rehearsal may not be necessary for primacy effects (Wright et al., 1990), a gustatory short-term store should be independent of verbal information. One way to demonstrate an independence from verbalizability is through the use of an articulatory suppression task, such as verbally generating random numbers during the delay, or repeating a word or phrase aloud (Baddeley, 2002). If participants memorized “red” or “white” wines, there is no need to invoke a new, separate memory construct. Additionally, the first wine presented in a list is often considered preferential compared to other wines, regardless of their quality (Mantonakis et al., 2009), and this may provide an explanation for why Johnson et al. found a primacy effect.

Another important issue to consider regarding the findings of Johnson et al. (2014) is the way trials were created. Because probe distractors were always novel stimuli, participants would never need to compare the probe to the 3-item list, but only whether the item was familiar in the context of the session. Accordingly, participants would never need to maintain the three list items in memory. Even if the three gustatory objects were stored in memory, flavor and olfaction were not controlled for, and participants could use these cues to form the basis of their recognition response. While Johnson et al. state that these data support a short-term memory that is distinct from visual, verbal, or olfactory cues, and that these serial-position effects are free from proactive interference, such claims are hardly conclusive.

In conclusion, previous studies have been unable to successfully demonstrate that individual tastants can be remembered after a short delay. Studies that purport to do so (such as those on expertise) fail to control for contributing effects of odor and flavor. Other studies that have participants remember one basic taste (e.g., Barker & Lewis, 1983) have discovered that participants are unable to retain perfect representations across a delay. These findings lead one to wonder if memory for taste may exist at all. However, if all other basic senses have evidence for short-term stores, it stands to reason that one would exist for taste, but why has it been so elusive? Is this because taste has the least amount of cortical space dedicated in the human brain (Chen, Gabitto, Peng, Ryba, & Zuker, 2011), or have experiments been unsuccessful in producing this evidence because of task-specific features? To address this gap in the literature, experiments will need to use more than one tastant during the memory task to minimalize any effect of relative intensity, and tastants will need to be free from any odor or flavor. The following set of experiments will take this into account to systematically explore taste short-term memory.

Chapter 2: Experiments

Experimental Overview

The following experiments sought to a) demonstrate recognition for taste-related stimuli and b) systematically investigate whether taste-related stimuli can create the effects of primacy, recency, or both. Experiment 1 found evidence for recognition memory for taste by using colorless, scentless liquids (tastants) in a single-item recognition task. A follow-up experiment (Experiment 1.1) slightly altered the stimulus set to increase the perceptual distance between bitter tastants. Memories for these basic tastes were not susceptible to a rehearsal suppression task, suggesting an independence from hypothesized components of the multi-component model of WM.

Experiment 2 expanded upon the findings of Experiment 1 by introducing multiple tastants to be remembered during the sample phase of the procedure. In Experiment 2, participants were required to temporarily maintain multiple tastants concurrently, one of the core principles necessary for the demonstration of working memory. These tastants were serially presented as a list of three liquids, allowing for the possibility of primacy or recency effects. With a 30-s delay, taste list memory produces as a recency effect, but with a 60-s delay (introduced in Experiment 2.1) taste list memory produces a primacy effect. These data show that not only is taste short-term memory independent from visual and verbal stores, but it is susceptible to the same interference processes that other modalities are.

Experiment 1

The goal of Experiment 1 was to test whether tastants could be temporarily stored over a delay. By having a single-item recognition task examine one tastant at a time, we examined the effects of hedonic value, intensity, and verbalizability on memory. The hedonic value, or how pleasurable the tastant is, can be a predictor of memory strength in odors and tastes, particularly if the tastant is aversive. The reported intensity of the tastant will record the saliency of the taste, and it will ensure that, within this study, no single stimulus is disproportionately stronger or weaker than others. The verbalizability of the stimulus will be informative when compared to accuracy in the recognition task. Previous research suggests that the verbalizability of a stimulus will result in different levels of recognition accuracy based on delay length, with non-verbal stimuli resulting in poorer accuracy at longer delays (Engen & Ross, 1973; Zelano et al., 2009).

One of the goals of the current study was to create a salient stimulus set. If one or more stimuli in the experiment created disproportionately higher, or poorer, accuracy, those liquid solutions would be altered until all stimuli were sufficiently different. This stimulus set would later be used in Experiment 2. An ideal stimulus set would result in recognition that is reliably above chance (50%), with accuracy being highest for tastants that are perceptually distinct (e.g., bitter and sweet), and accuracy lowest for tastants that are perceptually similar (e.g., varying degrees of sweetness). Participants performed a recognition task where they are required to remember one tastant at a time over a delay (DMTS). Afterwards, they rated the specific qualities of every individual taste involved in the study to measure and control for intensity, verbalizability, and hedonic value, analogous to Experiment 1 in Zelano et al. (2009).

Methods

34 participants were recruited from Auburn University's Sona system (https://auburn.sona-systems.com/), where undergraduate students enrolled in psychology courses are given the opportunity to participate in research in return for extra credit. Participants were recruited for times between 9AM and 5PM with an hour taken off at noon to avoid any contributing effects of lunch. Ages ranged from 18 to 23 (M = 18.4 years), with 23 of participants identifying as female, and 4 reporting that their left hand was their dominant hand. 4 participants withdrew mid-study after expressing disgust with the taste of the stimulus set, and their data is not included in the subsequent results. Total participation in this study lasted no longer than one hour.

Apparatus

Timing and data logging will be handled by E-Prime 2.0 Professional running on Windows XP. All programs were custom-written by the author. Participants read all instructions and trial events while seated 30-cm away from a 17-in LCD monitor (1280 x 1024, 60Hz). Responses were recorded with a keyboard and mouse.

All liquids were stored in small 5 mL semi-opaque plastic canisters with lids. 20-oz cups were provided for liquid waste disposal when participants were done with their tastants. Throughout the experiment, distilled water was provided in 20 oz bottles along with non-bendable straws.

Stimuli

All tastants were created by mixing distilled water with one of four ingredients to emulate the basic tastes of salty, sour, sweet, and bitter (Chandrashekar, Hoon, Ryba, & Zuker, 2006). Including these four basic tastes allows all liquids to be equally clear and without any flavor, so participants are not given additional cues to which to solve the task. Each basic taste will be varied along two dimensions so that 8 total liquid stimuli are created (e.g., Moderately Bitter, Very Bitter). Based on previous findings, the High concentration tastants Table 1 includes a full list of liquids to be used in the current study along with their ingredients and concentrations.

Taste	**Active Ingredient**	**Concentration (weight / volume)**
Moderately Sweet	Sucrose	4%
Highly Sweet	Sucrose	8%
Moderately Salty	Sodium Chloride	2%
Highly Salty	Sodium Chloride	4%
Moderately Sour	Citric Acid	5%
Highly Sour	Citric Acid	10%
Moderately Bitter	Quinine Hydrochloride	4%
Highly Bitter	Quinine Hydrochloride	8%

Table 1. The list of tastant labels, their active ingredients, and the concentration as measured by mg / L. All active ingredients were mixed with distilled water.

All stimuli were stored at room temperature, and all ingredients were mixed in advance to ensure solutions were well mixed or no longer carbonated (in the case of tonic water). None of these stimuli included ingredients that are common in food allergies, such as lactose, peanuts, or Red Food Dye No. 4. All tastants were created on the day of data collection.

Procedure

Memory Task. Participants entering the study were greeted by a researcher and asked to review an IRB-approved informed consent letter. After participants consented, the researcher reviewed the key points of the study to ensure that the participant is aware of what the current study requires of their participation. After being briefed, participants were directed to a computer, where they will answer a series of brief questions, including questions about: gender, age, handedness, food allergies, soda consumption, coffee consumption, and smoking habits. An exhaustive list of the questions asked in the beginning of this study can be found in Appendix A. Participants were informed that if they had any food allergies, they would not be allowed to continue in the experiment, but they would receive full credit for their participation. No participants disclosed having a food allergy of any kind. After answering this initial set of questions, the following set of instructions were displayed on the computer monitor:

> INSTRUCTIONS:
>
> In this task, you will taste a variety of liquids. Your goal is to remember the first liquid of each trial.
>
> For each trial, you will taste the liquid, and then spit it into the blue cup in front of you. After this, you will rinse your mouth with the distilled water and spit again in the blue cup. After a short 30-second delay, you will be given a second liquid. If this liquid was identical to the first liquid, press "F". If this liquid was NOT identical (in taste, intensity, or both) to the first liquid, press "D". If the two liquids are different in any way, please press “D”.
>
> During the delay, you will be asked to repeat the word "the" aloud until you are instructed to taste the second liquid. It is important that you repeat this word once a second until you taste the second liquid.

> There are a total of 16 trials in this portion of the experiment, lasting approximately 40 minutes. Once you are ready and comfortable with these instructions, please inform the researcher.

After participants finished reading the instructions, the researcher verbally described the experiment, pointing out the location of relevant apparatuses and demonstrating appropriate gestures. Participants were told to think of “D” as “for different”. Once participants had no further questions and reported being comfortable with the task instructions, they were allowed to continue.

Before each trial began, the computer presented a dialog prompt asking participants if they are ready to begin the next trial. When participants acknowledged that they were ready to continue via pressing the spacebar, the computer displayed text letting the participant know to immediately taste the liquid from the cup in front of them. Cups were always placed in front and to the left of participants before the beginning of each trial. When participants were finished tasting the liquid, they discharge the contents of their mouths into a cup. Following the computer’s visual instructions, participants tasted the sample stimulus for only 4 s. Directly after the sample presentation was discharged into the cup, the computer prompted participants to take a sip of water in order to rinse their mouths, and they discharged this too into the waste cup. Participants were advised to rinse and discharge a sip of distilled water as a palette cleanser to eradicate any trace amounts of the sample liquid (Johnson & Vickers, 2004). This palette cleansing lasted 4 s, and a delay of 30 s directly followed. This delay length was chosen based on findings of Wright et al. (1985) that demonstrated strong primacy and recency effects with 4-item lists for visual information. Additionally, this delay length produced the recency effect in a

4-item list of auditory stimuli with monkeys, a good model for nonverbal memory (Wright & Roediger, 2003). During this delay, participants repeated the word “the” aloud at least once a second for the entirety of the delay. Repeating the phrase “the” aloud is a rehearsal suppression technique that disrupts verbal rehearsal so that information is not temporarily stored through linguistic codes (Baddeley, 2002). If participants did not immediately begin repeating “the”, the researcher reminded them to continue to say “the” until the probe stimulus was tasted.

During the delay, the researcher placed the probe tastant in front of participants. With 2 s of the delay remaining, the computer prompted the participants to prepare to drink the probe liquid. After drinking the probe liquid, participants discharged the liquid into a spittoon and then responded via keyboard whether the two liquids were the “same” (by pressing “F”) or “different” (by pressing “D”). Feedback was provided after each response. In the event of a correct trial, the word “CORRECT” in blue font appeared, and in the event of an incorrect trial, the word “INCORRECT” appeared in red font. Response time and cumulative accuracy was also presented below their feedback. Feedback was provided to ensure that participants understood the dimensions of sameness or difference between stimuli; in other words, Moderately Salty and Highly Salty were presented, participants would understand that those tastes are scored as “different” trials. Each trial was followed by a 30-s intertrial interval before the next trial began, and during this time, participants rinsed and spat to clear any residual taste from the probe.

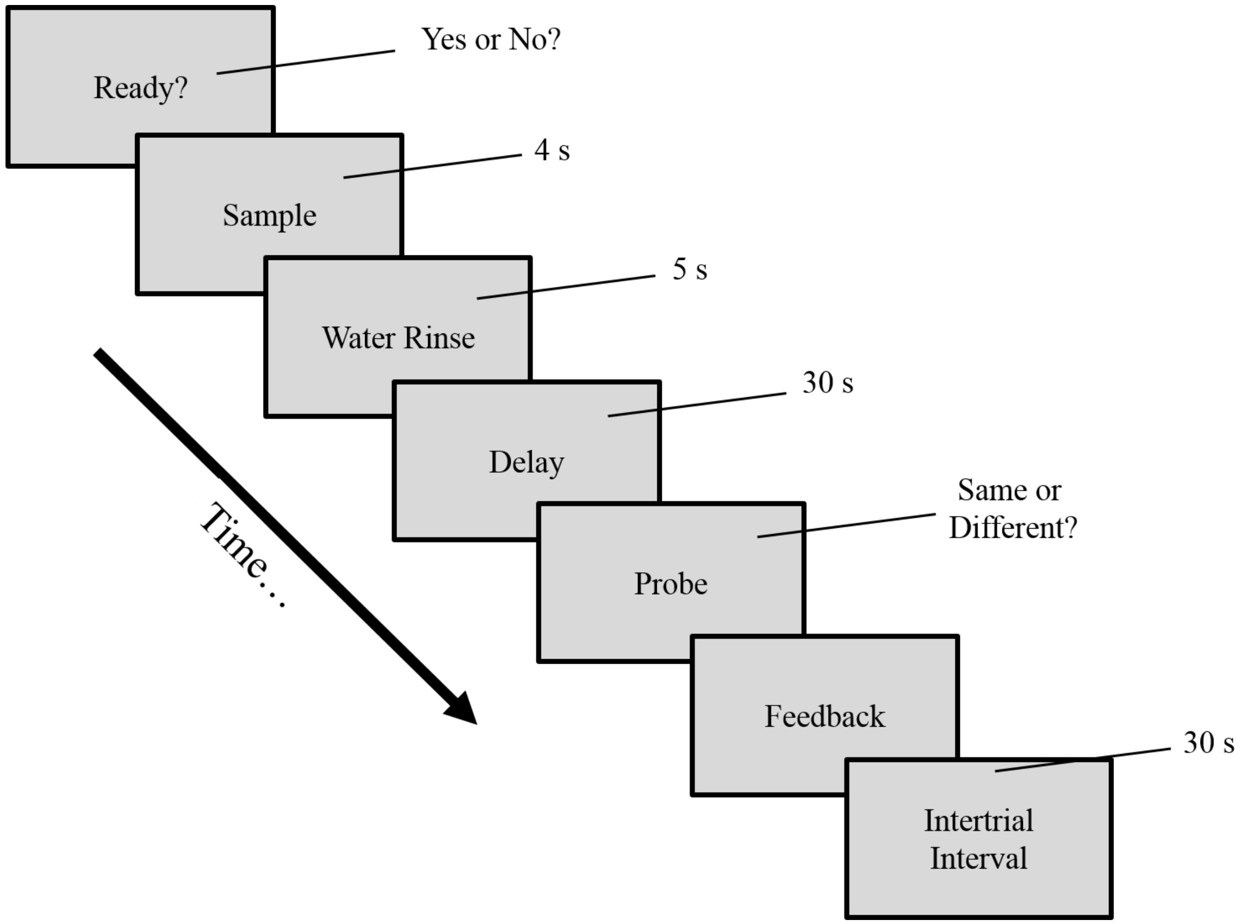

Figure 7. Trial progression for Experiment 1.

Each session contained 16 trials, where 8 trials were "same" discriminations and 8 trials were "different" discriminations. Tastants were pseudorandomly assigned before each session. The balance of "same" and "different" trials allowed each tastant to serve twice as the sample tastant, and once as the same comparison (i.e., a "same" trial). Each tastant also served once as the non-matching comparison (i.e., a "different" trial). Of the "different" trials, half of these trials were cross-taste comparisons (e.g, mildly sour and very salty) and the remaining four are within-taste comparisons (e.g., mildly sour and very sour). The tastants making up these cross-taste and within-taste trials were pseudorandomly assigned so that no two trials had the same within-taste discrimination. In other words, if one trial compared mildly bitter to very bitter, no subsequent trial would compare very bitter to mildly bitter. All trial ordering was randomized across participants.

When participants completed all trials in the recognition task, they were asked if they had any questions regarding the task they just completed and if they need a short break before continuing. When participants acknowledged that they were ready to continue, a short questionnaire was presented. The items on the questionnaire asked participants to explain how they solved the task and other similar task-related questions (see Appendix B). If participants used visual, tactile, or verbal cues, or any other strategy to successfully memorize a tastant, this questionnaire should show a systematic trend among participants. After participants completed writing for each question, the researcher asked them to sit in front of the computer once more to complete a series of self-report measures regarding the current stimulus set.

Ratings Task. Once seated at the computer, the following set of instructions appeared on the monitor:

> INSTRUCTIONS:
>
> For the next few minutes, you will taste a variety of liquids. After each taste, you will get have the opportunity to tell us how much you enjoyed that taste, how intense it was, and how easily you could put that experience into words.
>
> Like the previous task, you will taste a liquid, spit it into the blue cup, rinse with the distilled water, and spit again into the red cup. You will be able to respond using an on-screen slider with your mouse. There are only 9 trials, and this portion of the experiment lasts approximately 6 minutes. If you have any

questions, please let the researcher know now. Otherwise, you may continue.

Press any key to begin.

Once ready, participants used the computer's mouse to respond along a visual analog scale with ratings of 0 to 100 and no anchors (Zelano et al., 2009). For each trial, participants tasted a liquid used in the previous recognition task and then responded to how pleasant, how intense, and how easily verbalizable that liquid is. Regarding pleasantness, participants were instructed: "Using the scale below, please indicate how much you enjoyed the current taste," with 0 being "I hated this taste" and 100 being "I loved this taste." Regarding intensity, participants were instructed: "Using the scale below, please indicate how intense the current taste was," with 0 being "I could barely taste it" and 100 being "It was overwhelming." Regarding verbalizability, participants were instructed: "Using the scale below, please indicate how easily verbalizable the current taste is," with 0 being "I can think of no words to describe this taste" and 100 being "I can easily think of a word to describe this taste." Participants were presented with 9 total liquids in this task – 8 liquids were used in the current stimulus set, and 1 liquid was normal distilled water used as a control condition. Liquids were presented in a pseudorandomized order so that no basic taste was presented directly after itself; for example, "mildly bitter" and "very bitter" could not occur consecutively.

After completing the final trial of the taste ratings task, participants were debriefed and allowed to ask any questions they may have regarding the study. Bottled water was available for all participants upon their exit.

Data Analysis

Statistical analyses were performed using SPSS (Version 22.0; IBM, 2013) and R (Version 2.15.1; R Code Team, 2012). Power was assessed using G*Power (Version 3.0; Faul, Erdfelder, Lang, and Buchner, 2007), and moderate-to-large effects (i.e., η_{ρ}^{2} = .33) would require a sample size of 25 participants for sufficient power. Because proportions, such as accuracy, are not normally-distributed variables, results were transformed using the arcsine square root transformation. This transformation was applied to recognition accuracy on all following experiments so that traditional statistical tests do not violate assumptions of a normal sampling distribution (McDonald, 2014). The arcsine square root transformation reduces statistical power, but it provides greater interpretability for mean proportion data compared to logistic regression (Warton & Hui, 2011).

Experiment 1 Results

Recognition Task

Participants were able to successfully memorize tastants over a delay, as confirmed by a comparing overall mean performance of each participant against chance (50%; one-samples *t*-test $t(29) = 9.62$, $p < .01$, $d = 3.57$). Mean accuracy for the three trial types (Same, Within-Taste, and Between-Taste) of Experiment 1 are shown in Figure 8. Bonferroni-corrected one-samples *t*-tests found that accuracy for Same and Cross-Taste trials were significantly above chance, *t*s(29) > 5.42, *p*s < .01, *d*s > 2.02, but Within-Taste trial accuracy was equivalent to chance, $p = .015$. Additionally, a one-way repeated-measures Analysis of Variance (ANOVA) on trial type (Same, Cross-Taste Different, Within-Taste Different) found differences in accuracy across trial type, $F(2, 58) = 7.73$, $p < .01$, η_{ρ}^{2} = .201. Post-hoc pairwise comparisons follow-up tests showed that this difference is the result of poorer accuracy for Within-Taste discriminations compared to Cross-Taste and Same discriminations, *p*s < .01.

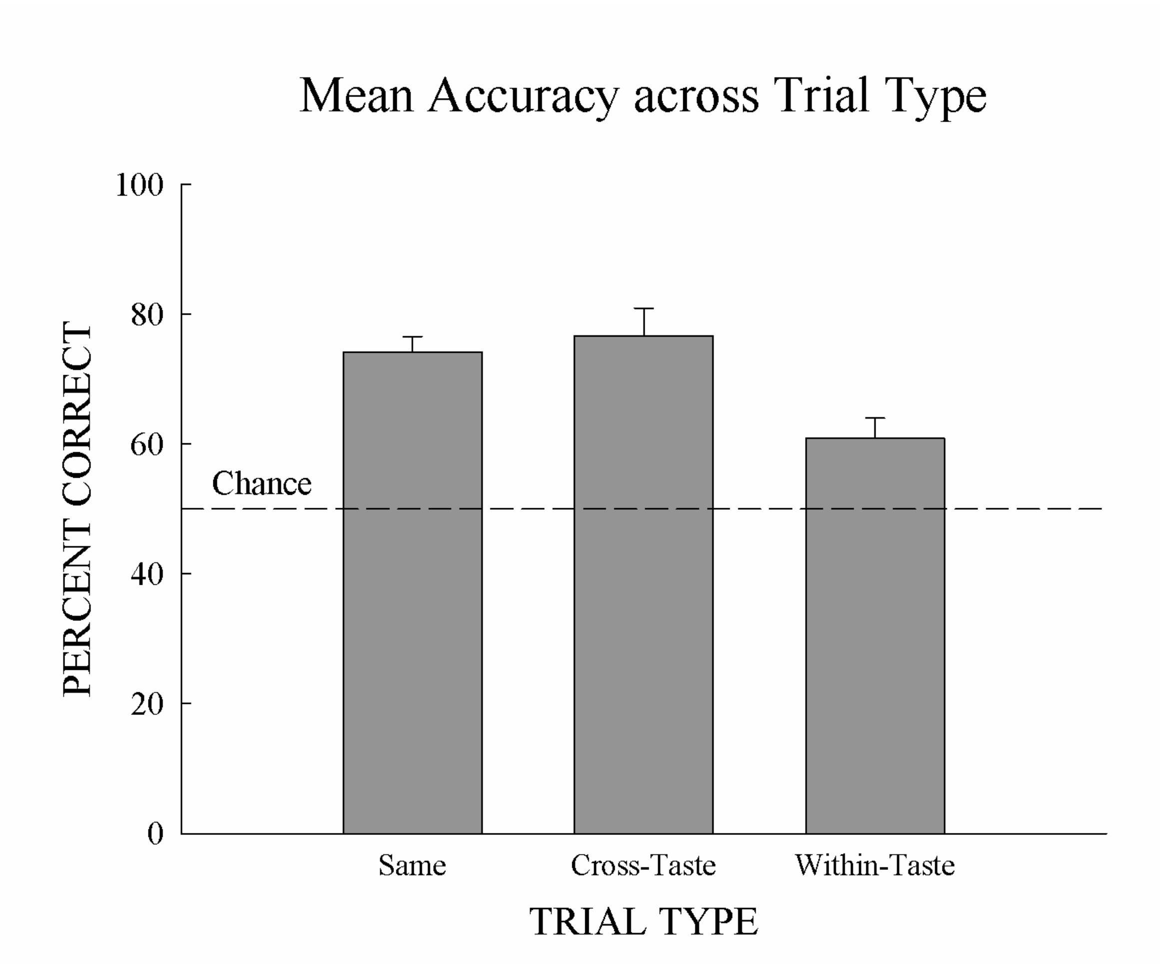

Figure 8. Accuracy across trial types for Experiment 1. Bars represent the different trial types, and the dashed line represents chance accuracy (50%). Both Same and Cross-Taste trials resulted in above-chance accuracy. Accuracy for Within-Taste trials was not above chance. Error bars represent standard error of the mean.

Within-Taste Trials. Mean accuracy for Within-Taste discriminations are shown in Figure 9. Participants were better at discriminating some tastes than others, and this was confirmed by a one-way repeated-measures ANOVA of Taste (salty, sweet, sour, bitter), $F(3, 42) = 6.314$, $p < .01$, $\eta_\rho^2 = .179$. Post-hoc pair-wise comparisons showed that this difference is due to poorer accuracy for Within-Taste bitter discriminations, and accuracy for these bitter trials were significantly worse than any other Within-Taste discrimination, *p*s < .05. Poor accuracy on the Within-Taste bitter discriminations was due to a bias to respond “same”; 22 out of 30 participants responded “same” when presented with a Moderately Bitter and Highly Bitter tastant. An exact binomial sign test indicated that this ratio was significantly different from chance, *p* < .05.

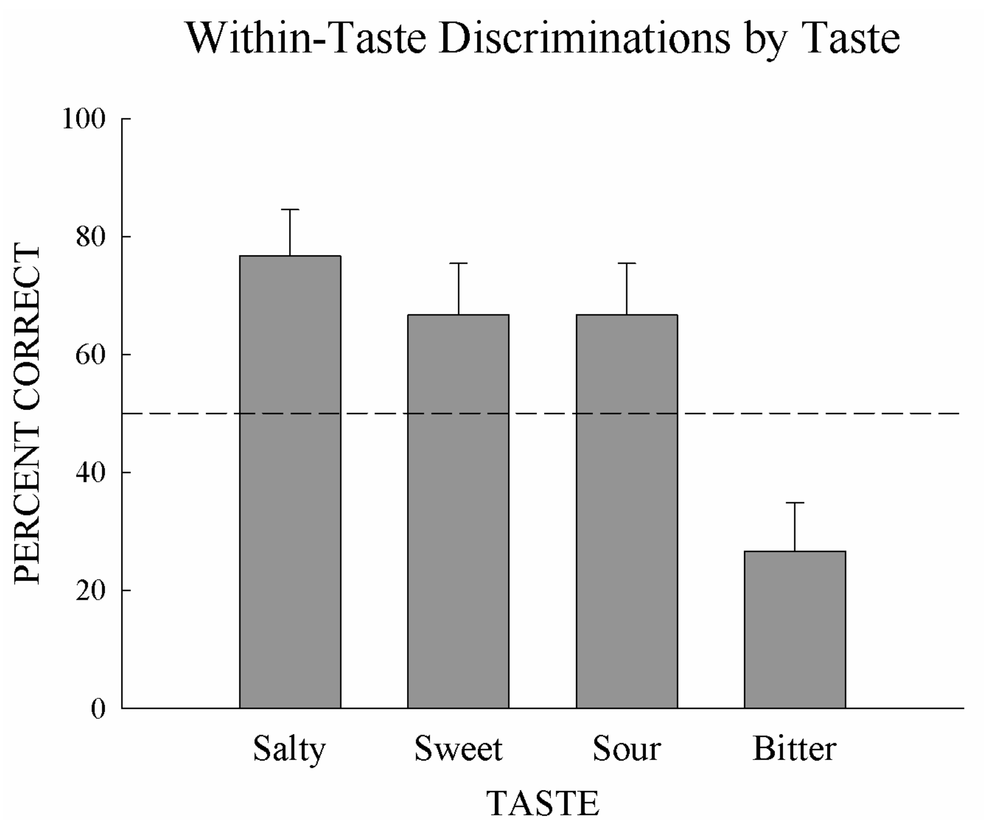

Figure 9. Accuracy for Within-Taste trials in Experiment 1. Bars represent the different tastes, and the dashed line represents chance accuracy (50%). Error bars represent standard error of the mean.

Trial Order. Mean accuracy across trials is shown in Figure 10. There was no effect of trial order, as confirmed by a one-way repeated-measures ANOVA, $F(15, 435) = 1.44$, $p = .13$. While accuracy did not significantly vary across trials, the first trial of each session is of particular interest as a comparison to other taste-recognition experiments (e.g., Barker & Weaver, 1983). A follow-up one-sample *t*-test showed that accuracy on the first trial was equivalent to chance, $t(29) = 0.36$, $p = .72$. Poor accuracy on the first trial was due to a bias to respond "different"; 20 out of 30 participants responded "different". An exact binomial sign test indicated that this ratio was significantly different from chance, $p < .05$.

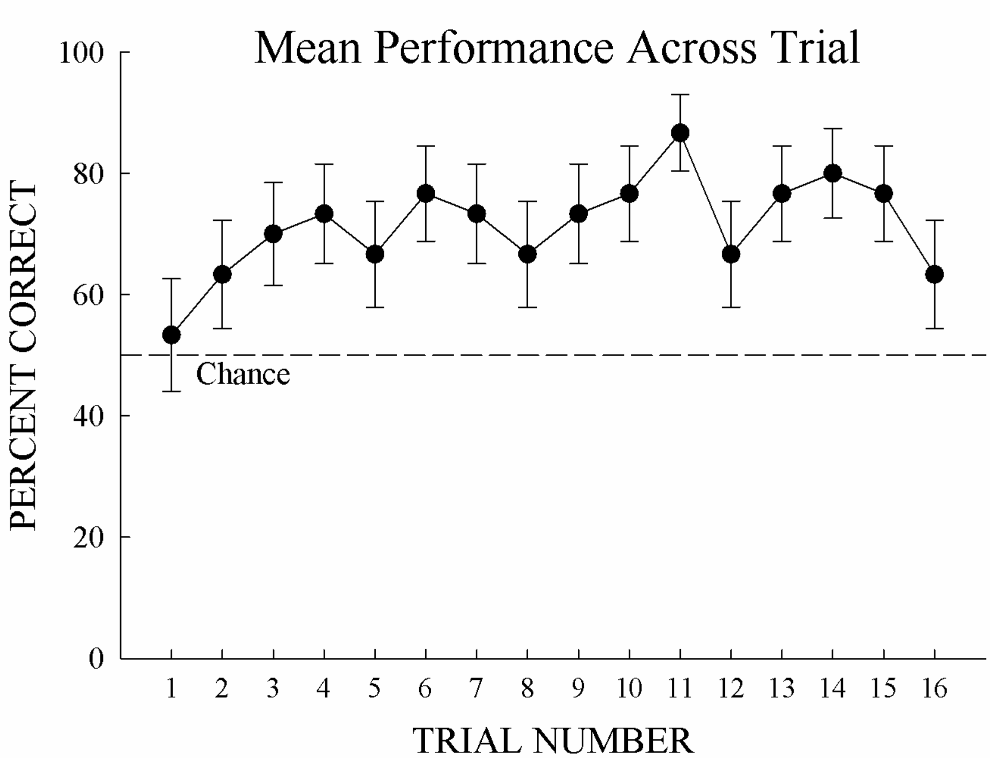

Figure 10. Mean accuracy across trial number. Accuracy did not systematically change across trial order. The first trial's accuracy was not above chance (50%). The dashed line represents chance accuracy, and the error bars represent standard error of the mean.

Post-Task Questionnaire. One participant reported feeling bored during the task, but no one reported finding themselves unable to pay attention during the task. Three participants reported that they felt “full” at the end of the experiment. When asked if there was a particular strategy that they used to remember the tastants, 21 participants responded with specifically nonverbal accounts: “I remembered the tastes,” or “Tried to remember the first taste of the trial,” for example. Four participants responded with strategies that may have had verbal components, such as “I tried to remember if it was sweet, sour, or mediocre” or “I remembered if it was strong or mild, or weak.” The remaining participants either declined to respond, stated that they had no strategy, or did not provide a relevant answer (e.g., “this stuff tastes terrible,” or “the extra credit will be worth this”).

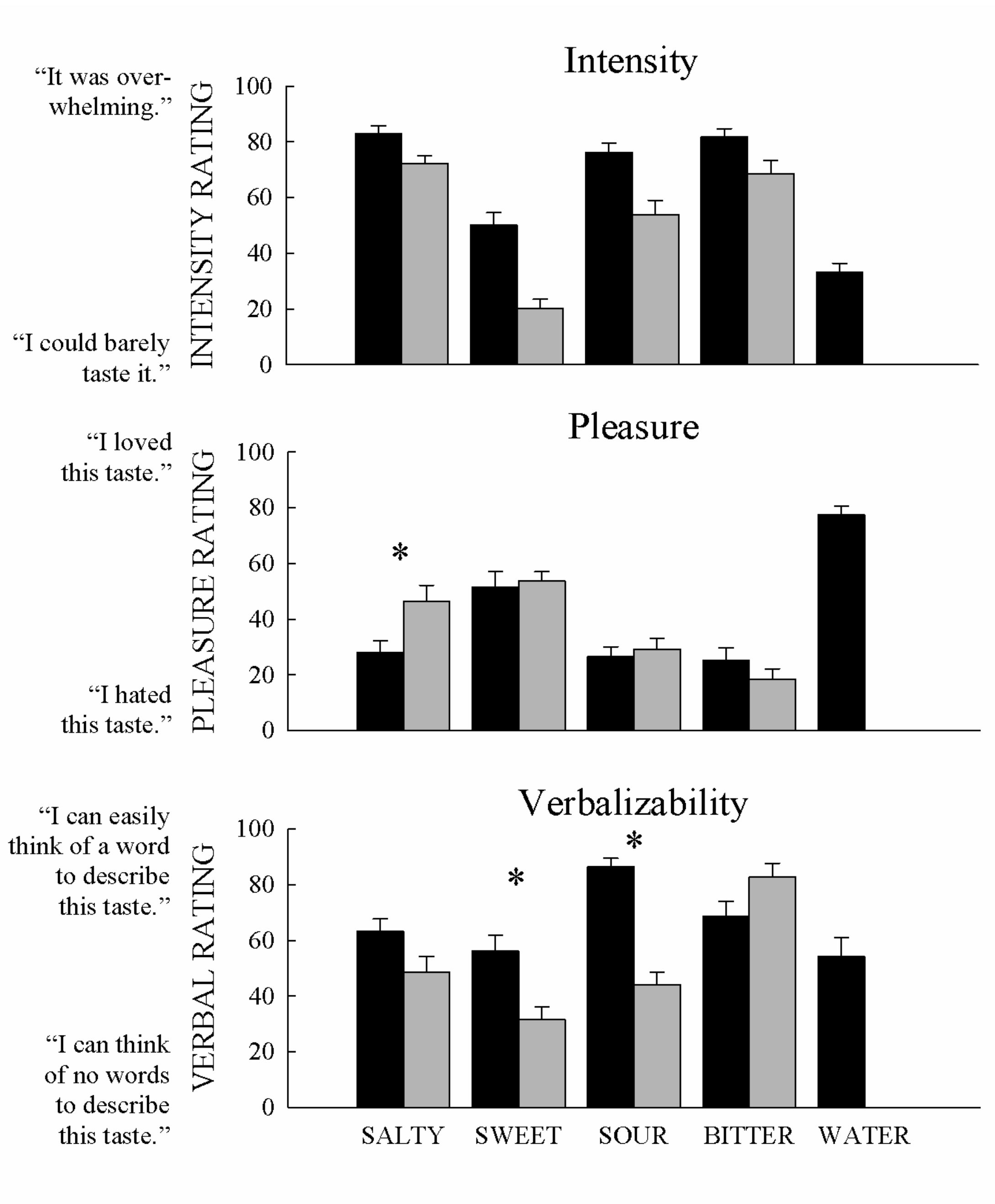

Figure 11. Mean ratings for each tastant, with black-filled bars representing high-concentrations and the grey-filled bars representing moderate-concentrations. The top panel represents the reported intensity of each tastant. The middle panel represents the reported pleasure of each tastant. The bottom panel represents the reported verbalizability of each tastant. Asterisks show significant differences as reported by paired-samples t-tests. Error bars represent the standard error of the mean.

Taste Ratings

Figure 11 shows the mean intensity, pleasure, and verbalizability ratings respectively for all participants. Tastants used in Experiment 1 varied in intensity (top panel of Figure 11). This was confirmed with a two-way repeated measures ANOVA of Taste (sweet, salty, bitter, sour) X Concentration (moderately, highly), that found a main effect of Taste $F(3, 87) = 55.85$, $p < .01$, $\eta_\rho^2 = .658$, and a main effect of Concentration, $F(1, 29) = 58.73$, $p < .01$, $\eta_\rho^2 = .666$, but no interaction, $p = .06$. Participants rated high concentrations (e.g., highly bitter, highly salty) as more intense than moderate concentration tastants. Bonferroni-corrected post-hoc tests showed that the main effect of Taste was largely due to participants rating sweet tastants as less intense than all other tastants, *p*s < .01.

Tastants used in Experiment 1 varied in pleasure (middle panel of Figure 11). This was confirmed with a two-way repeated-measures ANOVA of Taste X Concentration, finding a main effect of Taste, $F(3, 87) = 15.54$, p < .01, $\eta_\rho^2 = .35$ no effect of Concentration, and an interaction between the two factors, $F(3, 87) = 3.32$, $p < .05$, $\eta_\rho^2 = .1$. Bonferroni-corrected post-hoc tests showed that the main effect of Taste is largely due to participants rating sweet tastants higher than all others, *p*s < .01. Bonferroni-corrected post-hoc paired-samples *t*-tests showed that the interaction was due to participants rating Moderately Salty tastants as more pleasurable than Highly Salty tastants, $t(29) = 2.97$, $p < .01$, $d = 1.1$, and no differences between concentration levels for each of the other tastes.

Tastants used in Experiment 1 varied in verbalizability (bottom panel of Figure 11). This was confirmed with a two-way repeated-measures ANOVA of Taste X Concentration, finding a main effect of Taste, $F(3, 87) = 15.65$, $p < .01$, $\eta_\rho^2 = .351$, a main effect of Concentration, *F*(1,

29) = 28.72, $p < .01$, $\eta_\rho^2 = .498$, and an interaction between the two factors, $F(3, 87) = 9.87$, $p < .01$, $\eta_\rho^2 = .254$. Bonferroni-corrected post-hoc *t*-tests showed that this interaction is due to participants rating sweet tastants as less verbalizable than sour and bitter tastants, *ps* < .05, and bitter tastants as more verbalizable that sweet and salty tastants *p*s < .05. Additional Bonferroni-corrected post-hoc *t*-tests showed that the interaction was due to participants rating Highly Sweet and Highly Sour tastants as more verbalizable than Moderately Sweet and Moderately Sour tastants, respectively, *t*s(29) > 3.71, *p*s < .01, *d* = 1.38, and no differences between concentration levels for each of the other tastants.

Predicting Accuracy with Taste Ratings. To examine the contributions of intensity, pleasure, and verbalizability on accuracy, individual participants' Taste Ratings were paired to their DMTS results (cf. Zelano et al., 2009). Each trial was assigned an intensity, pleasure, and verbalizability score based on the sample and probe used. Ratings were not meaned or collapsed across participants in order to allow for a test that would be sensitive to individual differences in taste perception. Because the outcome of a DMTS trial is discrete (i.e., correct or incorrect), logistic regression was used to model the data.

Overall, this model did not predict accurate responses, so the probability of a participant making a correct response on a trial was independent of their ratings of intensity ($p = .74$), pleasure ($p = .55$), and verbalizability ($p = .12$). Figure 12 shows the lack of predictive value afforded by verbalizability ratings, with ratings of 100 depicted in the top line and of 0 in the bottom line.

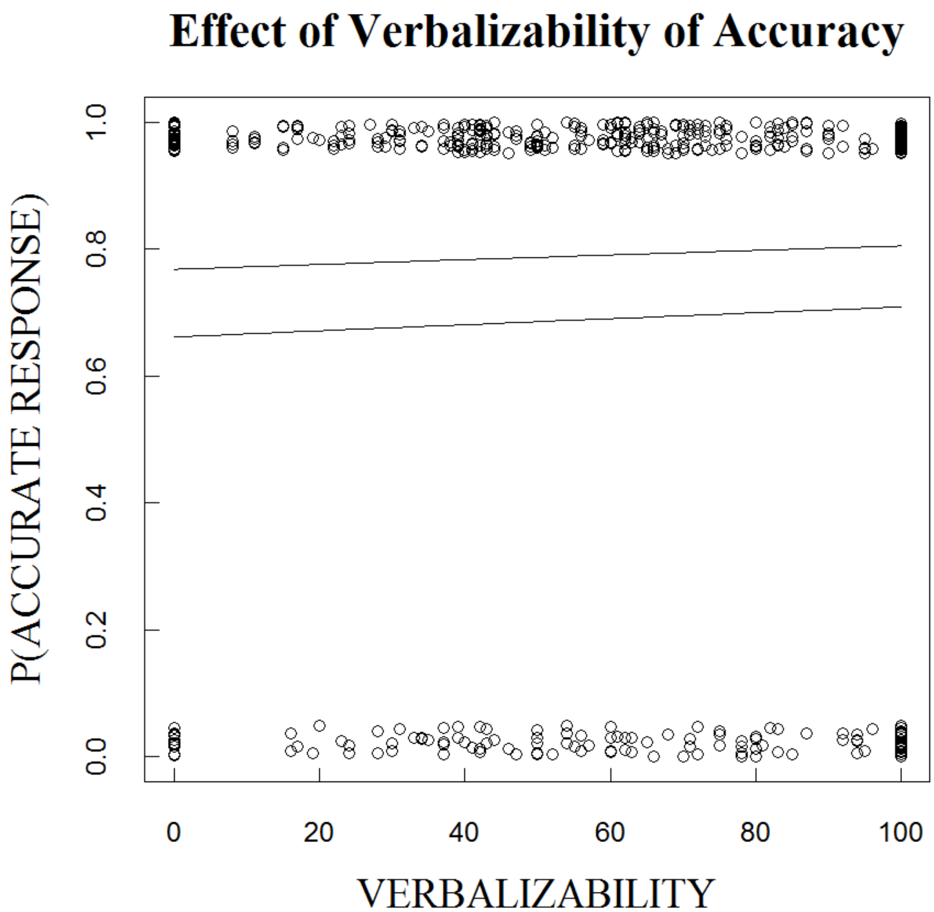

Figure 12. Individual plot for one factor of the three-factor logistic regression. Participants' ratings of individual participants' verbalizability did not predict the probability of making an accurate response. Lines reflect the effect on accuracy for tastants with a verbalizability rating of 100 (top line) and 0 (bottom line).

A post-hoc correlations test found that all three factors measured in the Taste Ratings task were highly related. As intensity ratings increased, so too did verbalizability ($r = .15$, $p < .05$), but pleasure ratings decreased ($r = -.31$, $p < .05$). As ratings for pleasure increased, ratings decreased for both intensity and verbalizability ($r = .11$, $p < .05$). Effect sizes for these correlations were weak, with r^2 values < .09.

Experiment 1 Discussion

The results of Experiment 1 show that tastants can be briefly stored in WM. Because of the implementation of articulatory suppression, it is unlikely that participants were using verbal rehearsal to recognize the probe tastant. This contradicts the revised Baddeley (2012) model of WM that proposes taste is mediated in WM by language. The perceptual qualities of taste do not need to be recoded into verbal or lingual codes in order to be stored in WM. Instead, these results suggest that WM for taste is robust enough to withstand a brief distractor task such as saying the word "the" multiple times. Post-questionnaire results from participants confirm these findings, with no participants reporting the use of an explicitly verbal strategy to solve the task. A large percentage of participants reported trying to "remember the taste" over the delay (50%). Additionally, no participants reported using visual or tactile cues to determine the correct response.

Further evidence against the proposition that language mediates WM is the lack of predictive value verbalizability held on accuracy. Participants had the opportunity to rate how easy or difficult each tastant was to put into words. Even though participants did rate tastes differentially (see the above Figure 12), this had no effect on how likely they were to get a trial correct. If the episodic buffer mediated taste information through verbal or lingual codes, verbalizability should have been predictive of recognition accuracy, with highly verbalizable tastants making a trial easier to solve than others.

Other tastant-specific cues, such as intensity and hedonic value (i.e., pleasure), were not predictive of trial accuracy. This is important for two reasons. First, even though some tastants were rated as more pleasant or more intense than others, this did not affect how likely these tastants were recognized compared to others. If participants were able to discriminate tastants solely on the basis of pleasure or intensity, there would be no need to invoke a new WM construct to explain these findings because participants would only simply need to recognize if one stimulus is more or less intense or pleasurable than another stimulus. A representation of the tastant's identity would not be necessary in this case, but only its relationship with the previous tastant. Second, if varying levels of intensity or pleasure affected the outcome of a trial, serious consideration of the current stimulus set would be warranted in order to proceed with additional experimentation. These three factors may still influence performance during DMTS, but logistic regression has been shown to be a more powerful alternative to binomials or arcsine transformations (Gelman & Hill, 2009; Warton & Hui, 2011), making contributing effects of these factors negligible in the following experiments.

The results of Experiment 1 are counterintuitive in light of Barker and Weaver's (1983) findings. Because Barker and Weaver found no evidence for a stable representation of taste in memory, one might assume that participants in Experiment 1 would disproportionately respond "different" to the task. Indeed, this was the case for the first trial of the current study's sessions, with participants more often reporting that the probe stimulus was "different" from the sample. Based on this finding, future research in taste memory should consider allowing participants a warm-up trial to calibrate their discrimination. This initial propensity to respond "different" when given two tastants may have influenced the results of Barker and Weaver. There are several reasons why the current study deviates from Barker and Weaver's findings that taste does not have absolute representation in memory: 1) Barker and Weaver asked participants to make a single intensity judgment rather than a series of binary recognition responses, 2) the delay used by Barker and Weaver ranged from 1 min to 72 hrs compared to Experiment 1's 30-s delay, and

3) the stimulus set used in the current study is much larger than the one used in Barker and Weaver.

Before examining effects of list position on taste recognition (Experiment 2), it is necessary to calibrate the current stimulus set to achieve adequate discrimination across all Within-Taste trials.

Experiment 1.1

The stimuli used in Experiment 1 were 8 tastants created to be perceptually distinct from one another. In the case of sour, sweet, and salty, participants could reliably discriminate between different concentrations after a delay. For bitter tastants, participants were unable discriminate between 8% quinine hydrochloride and 4% quinine hydrochloride. Before advancing to Experiment 2, the concentration of quinine hydrochloride for the Mildly Bitter tastant was decreased in an attempt to create a larger perceptual distance between the two bitter tastants.

Experiment 1.1 Methods

An additional 11 subjects were recruited from Auburn University's Sona system (https://auburn.sona-systems.com/). Participants were recruited for times between 9AM and 5PM with an hour taken off at noon to avoid any contributing effects of lunch. Ages ranged from 18 to 20 (M = 18.6 years), with 8 of participants identifying as female, and 1 reporting that their left hand was their dominant hand. 1 participant declined to continue the study after the first trial. Total participation in this study lasted no longer than one hour.

The stimulus set used in Experiment 1 was used again with one exception; the Moderately Bitter tastant was created by the solution to 2% mg/L. The Highly Bitter tastant remained at 8% quinine hydrochloride. See Table 2 for a full list of stimuli used. All sessions contained at least one bitter Within-Taste trial, so that Moderately Bitter and Highly Bitter discriminations were recorded for each participant. All other details of Experiment 1 were repeated for Experiment 1.1

Taste	Active Ingredient	Concentration (weight / volume)
Moderately Sweet	Sucrose	4%
Highly Sweet	Sucrose	8%
Moderately Salty	Sodium Chloride	2%
Highly Salty	Sodium Chloride	4%
Moderately Sour	Citric Acid	5%
Highly Sour	Citric Acid	10%
Moderately Bitter	Quinine Hydrochloride	2%
Highly Bitter	Quinine Hydrochloride	8%

Table 2. The list of tastant labels, their active ingredients, and the concentration as measured by mg / L. Not the difference in the Moderately Bitter concentration compared to Table 1. All active ingredients were mixed with distilled water.

Experiment 1.1 Results and Discussion

Participants were able to successfully memorize tastants over a delay, as confirmed by a comparing mean performance of each participant against chance (50%; one-samples t-test against chance, $t(9) = 3.13$, $p < .01$, $d = 2.09$). Mean accuracy data the three trial types (Same, Within-Taste, and Between-Taste) of Experiment 1.1 are shown in Figure 13. Subsequent one-samples *t*-tests found that accuracy for all trial types was significantly above chance, $ts(9) > 2.5$, $ps < .037$, $d = 1.67$.

With the updated stimulus set, participants were able to briefly store representations of taste in memory across the 30-s delay. This finding replicates the evidence of Experiment 1, that working memory for taste exists and is distinct from verbal coding. Important for this study, however, is the comparison of the different trial types. A one-way repeated-measures Analysis of Variance (ANOVA) on trial type (Same, Cross-Taste Different, Within-Taste Different) found no differences in accuracy across trial type, $F(2, 18) = 0.53$, $p = .6$, $\eta_{\rho}^{2} = .05$. These data further showed that the effect of trial type found in Experiment 1 was largely due to the poor accuracy of Within-Taste trials. By changing the concentration of tonic water in the "mildly bitter" solution, participants were better able to discriminate Moderately Bitter and Highly Bitter tastants, resulting in an increase in accuracy for Within-Taste trials.

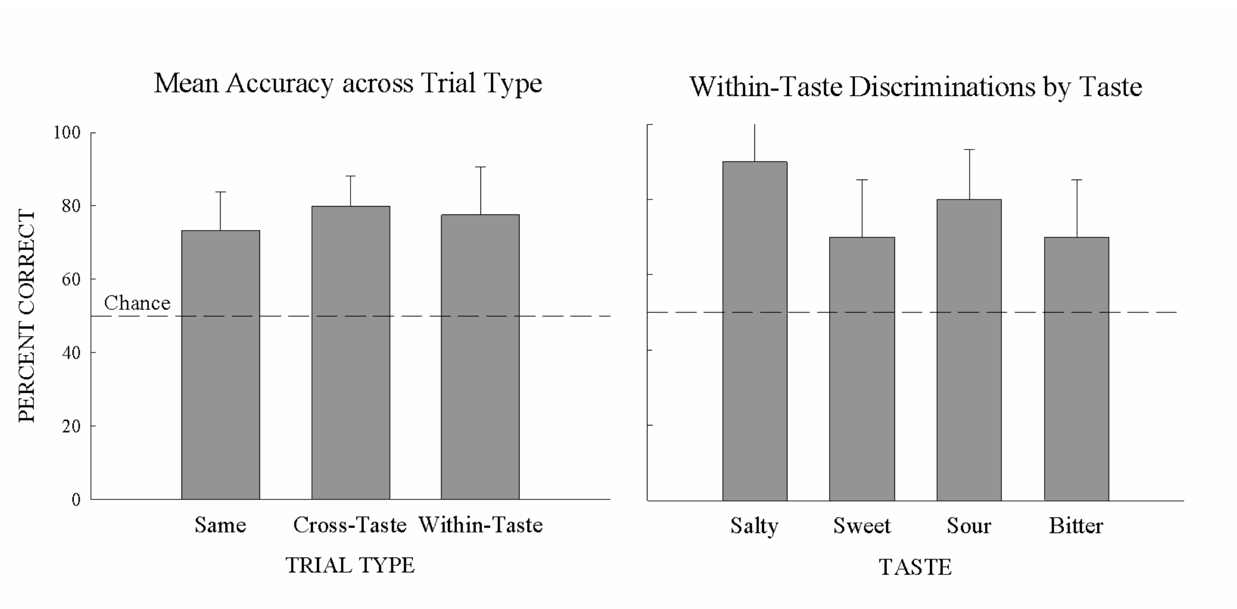

Figure 13. Panel A: mean accuracy across trial type. Accuracy was equivalent for all three trial types and reliably above chance (50%). Panel B: mean accuracy for Within-Taste trial types. Compared to Experiment 1, bitter discriminations were not below chance. The dashed line represents chance accuracy, and the error bars represent standard error of the mean.

Mean accuracy for Within-Taste discriminations are shown in the right panel of Figure 13. Participants performed equally well on discriminations for Within-Taste trials, as confirmed by a one-way repeated-measures ANOVA of Taste (salty, sweet, sour, bitter), $F(3, 27) = 0.452$, $p = .72$, $\eta_\rho^2 = .04$. In Experiment 1, a main effect showed that participants performed differently across the tastants used in Within-Taste trials, and post-hoc comparisons indicated that participants performed most poorly with bitter tastants. The difference in solution concentration between "mildly bitter" and "very bitter" was not large enough, and participants mistook these different tastants as being identical. In Experiment 1.1, the "mildly bitter" solution was diluted, creating a larger perceptual distance between these two tastants.

Experiment 2

The goal of Experiment 2 is to test list memory for gustatory objects. Expanding on the previous experiments, Experiment 2 increased the sample from a single tastant to a list of 3 tastants. With a 3-item list of tastants, participants would be required to encode and store multiple tastants in short-term memory. In order for participants to successfully complete a trial, the recognition probe would need to be compared to three possible tastants. The ability to store and manipulate information is a hallmark of WM, but WM must also be able to combat interference (Baddeley, 2002). If taste list memory is similar to visual list memory then effects of primacy and recency will result from interference within and between trials. A list of 3 tastants is large enough to allow for a U-shaped function, if accuracy is highest at list positions 1 and 3, creating both primacy and recency. Interference theory would predict that this middle tastant in list position 2 would receive the lowest accuracy of the 3 positions because of the deleterious effects of proactive and retroactive interference neither (Wright, 1998).

Another possible outcome of Experiment 2 is that only primacy or recency is found, but not both. For example, Johnson, Volp, and Miles (2014) found only primacy in their 3-item wine lists, although this conclusion should be qualified, as above mentioned. Wright (1998) discovered differences in serial-position effects for auditory and visual lists. Holding delay-length constant at 30 s, visual lists showed strong primacy, but auditory lists showed just the opposite, with recognition accuracy highest in the final list position. Finally, olfactory lists also show recency (White & Treisman, 1997; White, 1998), with little-to-no evidence for primacy. Due to the varied outcomes of these individual modalities, it is difficult to predict if Experiment 2 will result in primacy or recency. However, if a taste short-term memory exists, it will be susceptible to proactive and retroactive interference, creating serial-position effects.

Experiment 2 Methods

Participants

20 participants were recruited from Auburn University's Sona system. Students that participated in either Experiment 1 or Experiment 1.1 were not eligible for the study. Similar to previous experiments, participants were recruited for times between 9AM and 5PM with an hour taken off at noon to avoid any contributing effects of lunch. Ages ranged from 18 to 22 (M = 19.1 years), with 17 participants identifying as female, and 4 reporting that their left hand was their dominant hand. Total participation in this study lasted no longer than one hour.

Stimuli

The same stimuli used in Experiment 1.1 were used in Experiment 2. Table 2 offers the ingredients and concentration for each of the 8 tastants.

Procedure

Participants went through the same briefing process as Experiments 1 and 1.1. After reading and signing the informed consent, participants were seated and given instructions for the upcoming task.

> INSTRUCTIONS:
>
> In this task, you will taste a variety of liquids. Your goal is to remember a list of three liquids on each trial.
>
> For each trial, you will taste three liquids from the cups placed in front of you to your left. After you taste each liquid, you will then spit it into the blue cup in front of you. Once you've tasted all three liquids, you will rinse your mouth with the distilled water and spit again in the blue cup. After a short 30-second delay, you will be given a fourth liquid. If this liquid was identical to one you tasted in the list, press "F". If this liquid was NOT identical (in taste, intensity, or both) to the first liquid, press "D". If the fourth liquid is different from any of the earlier three in any way, please press "D".
>
> During the delay, you will be asked to repeat the word "the" aloud until you are instructed to taste the fourth liquid. It is important that you repeat this word once a second until you taste the fourth liquid.
>
> There are a total of 16 trials in this portion of the experiment, lasting approximately 40 minutes. Once you are ready and comfortable with these instructions, please inform the researcher.
>
> Press the spacebar to begin.

When participants acknowledged that they had read and understood the instructions, the researcher reviewed the task verbally. After participants confirmed with the researcher that they understood the instructions. After completing the instructions, participants were asked if they had any questions, and if they did not, they began the session.

At the start of each trial, a 3 liquids were placed to the left of the participant, and they were told to taste the liquid closest to them first, the middle liquid second, and the liquid furthest from them last. Participants acknowledged that they were ready for the next trial by pressing the spacebar on the keyboard. At the beginning of each trial, the computer presented the following visual instructions in order: “Please taste the first sample liquid. (4 Seconds)”, “Please taste the second sample liquid. (4 Seconds)”, and “Please taste the third sample liquid. (4 Seconds)”. During this time, participants grasped the corresponding liquid with their left hand, poured the tastant in their mouths, and discharged in an available cup in the right hand. After tasting all three liquids, participants rinsed and discharged with distilled water through a plastic straw. After rinsing, participants were instructed to say the word “the” once a second for the entirety of the 30-s delay. If participants did not immediate verbally rehearse the word “the”, the researcher reminded them to say “the” aloud. During this delay, the researcher removed the emptied cups from in front of the participants and replaced them with a fourth liquid serving as the recognition probe. With 2 s of the delay remaining, the computer presented a warning that the moment to taste the probe liquid was approaching.

Once prompted, participants tasted the probe liquid for 4 s before discharging. Visual instructions reminded the participants to respond “F” if the probe liquid was present in the 3-item list at the start of the trial and to respond “D” if the probe liquid was not present in the current list. After making their response, participants were given visual feedback as to whether their response was correct or incorrect along with their session's cumulative accuracy. Feedback lasted 4 s, with a 30-s intertrial interval following. During this ITI, participants rinsed and spat and waited for the next trial. While participants were told they could take a break between trials, no one waited longer than 30 s to begin the next trial.

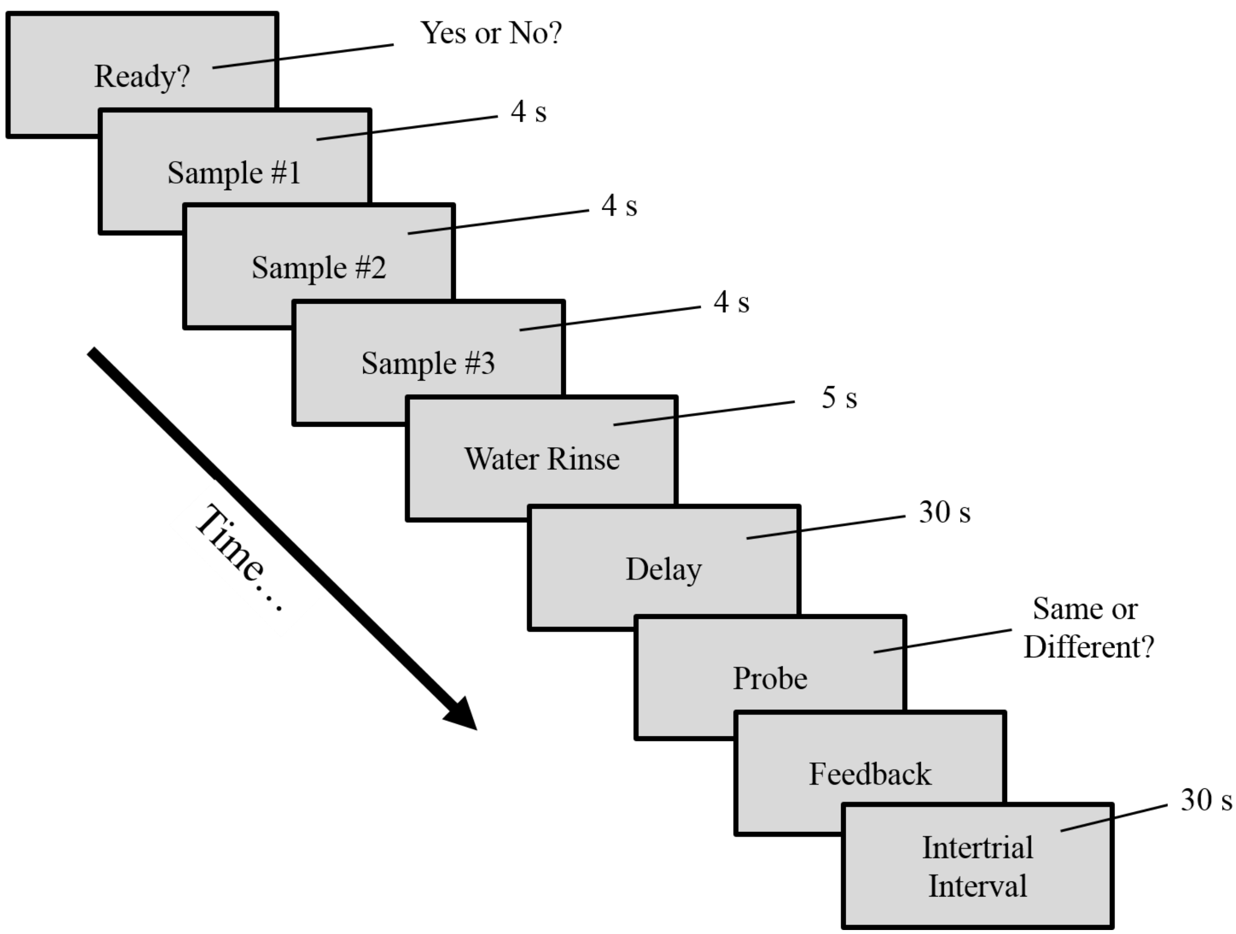

Figure 14. Sample trial progression for Experiment 2.

The recognition task increased the number of samples presented during a single trial from 1 to 3 (see Figure 14 for a trial progression). As with Experiments 1 and 1.1, 8 trials resulted in a "same" probe, and the remaining 8 will result in a "different" probe. For "same" trials, the probe tastant will have also been presented as one of the trial's 3 tastants. For "different" trials, the probe tastant will be one of the 5 tastants that was not presented as one of the trial's 3 tastants. Unlike Experiments 1 and 1.1, "different" trials were not split between Within-Taste and Between-Taste categories. Tastants were pseudorandomly assigned so that each tastant appeared exactly 8 times each session – 4 instances in "same" trials and 4 in "different" trials. Each tastant served as a "different" and "same" probe once. Each list position resulted in a corresponding "same" probe at least twice, and the remaining 2 "same" trials were randomly assigned as a one of the three list positions. Trials in which the "same" probe was originally presented in list position 1 will hereby be referred to as a "prime" trial, list position 2 as a "middle" trial, and list position 3 as a "recent" trial.

Experiment 2 Results

Participants were able to successfully discriminate between probe stimuli that did and did not appear in the sample list; recognition accuracy was significantly above chance (50%) as confirmed by a one-sample *t*-test, $t(19) = 7.03$, $p < .01$, $d = 3.23$. Accuracy was above chance for both "same" and "different" trials, $ts(19) > 4.44$, $ps < .01$, $d = 2.04$, and participants performed equally well on both trial types, as confirmed by a paired-samples *t*-test, $t(19) = .446$, $p = .66$, $d = 0.2$.

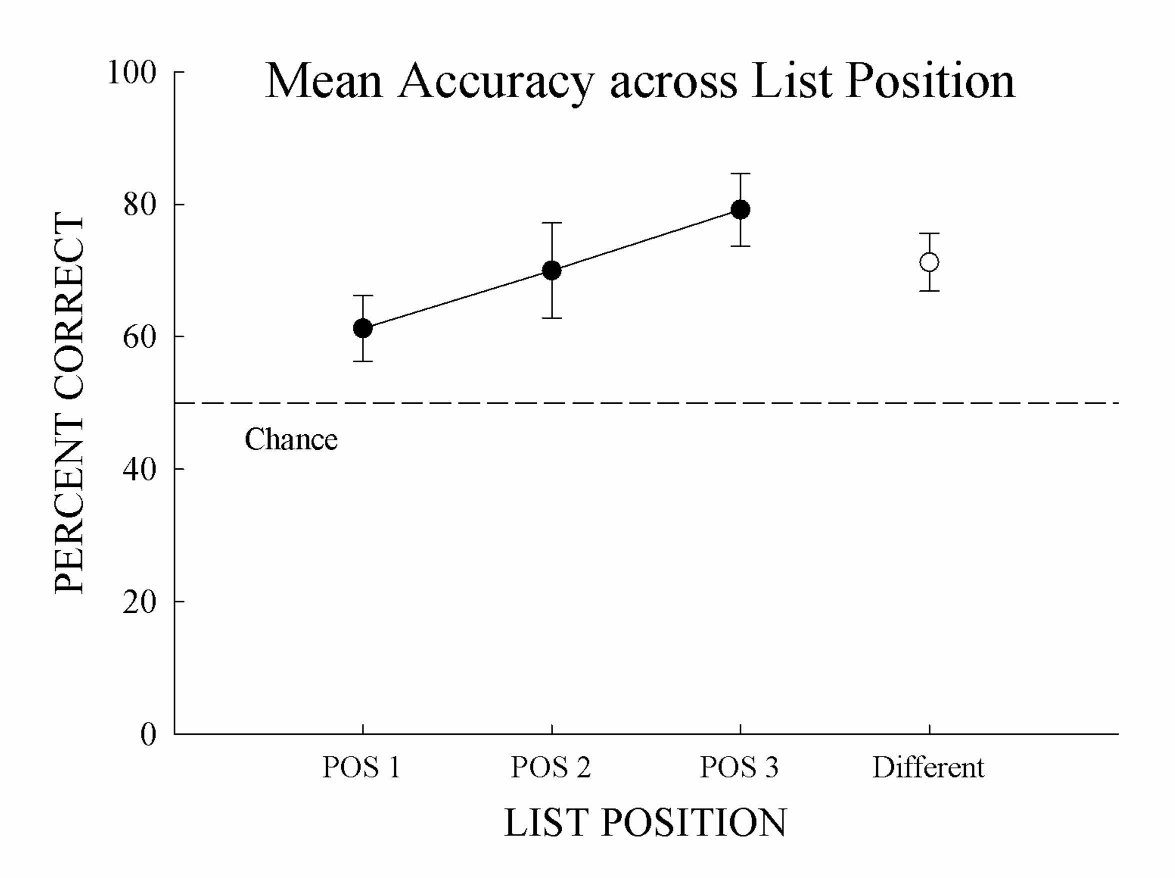

Figure 15. Mean percent correct for "same" trials (filled symbols) and "different" trials (open symbol). Participants demonstrated a recency effect, with accuracy of "same" trials the highest with probes originally presented in list position 3. Chance is represented by the dashed line, and error bars represent the standard error of the mean.

Figure 15 shows mean recognition accuracy across list position. To analyze the form of the serial position function, list position slopes were calculated for each participant and tested against 0. A one-sample *t*-test showed that the mean slope (14.6%) for recognition accuracy increased with list position, $t(19) = 3.24$, $p < .01$, $d = 1.49$. A one-way repeated measures ANOVA of List Position (1, 2, 3) did not detect a main effect, $p = .08$. However, polynomial contrasts showed that accuracy held a positive linear relationship across list position, $F(1, 19) = 10.52$, $p < .01$, $\eta_\rho^2 = .356$. This finding was confirmed with Bonferroni-corrected pairwise comparison *t*-tests that showed that accuracy was significantly higher on list position 3 compared to list position 1, $p < .05$. Accuracy did not differ between list positions 1 and 2 or list positions 2 and 3.

Post-Task Questionnaire. Two participants reported feeling bored during the task, and of these 2, 1 reported finding themselves unable to pay attention during the experiment. Two participants reported that they felt "full" at the end of the experiment. When asked if there was a particular strategy that they used to remember the tastants, 12 participants responded with accounts that were not specific to verbal labels: "I remembered what I tasted before," "I tried to remember what the three tastes tasted like," and "I tried to remember how strong it was and what it tasted like", for example. One participant reported thinking they could see a visual difference between the three tastes, and 3 participants responded with strategies that may have had verbal components, such as "I would try to associate the four basic tastes with each other" or "I remembered the strength of the taste." These participants' responses indicate some awareness that the stimuli could be turned into a word or phrase that could be compared to other stimuli within a trial. The remaining participants either declined to respond or stated that they had no strategy. All other participants reported having no strategy or "N/A".

Experiment 2 Discussion

According to Baddeley (2000), working memory is the ability to briefly store and manipulate information. In the current study, participants were not only able to withhold lists of tastes in memory over a brief delay, but they were able to later compare a fourth taste to this list of tastants. Participants were able to do this while inhibiting effects of a verbal distractor task and while combating effects of proactive and retroactive interference. These data suggest that a separate, independent short-term memory store for taste exists in human memory. According to

Baddeley's account of the episodic buffer, gustatory information would be coded as an efficient verbal code, but there is no evidence of such encoding was the basis for participants' discrimination in Experiments 1 or 2.

Experiment 2's results are contrary to the findings of Johnson, Volp, and Miles (2014). With 3-item lists of wine, participants' recognition was best for wines presented in list position 1. This demonstration of primacy is the opposite trend of the current study, where recognition was strongest for tastants in list position 3. These differences could be due to a number of distinctions between the two studies. First, instead of using an easily verbalizable substance like wines, the current study used tastants that were not easily nameable, thus reducing the likelihood of verbal rehearsal as a mechanism for recognition. Second, Johnson et al. did not attempt to prevent verbal rehearsal during the delay, unlike the articulatory suppression used here. Third, probe delays differed between the studies, with Johnson et al. using 5-s delays and the current study using 30-s delays. And fourth, Johnson et al.'s "different" trials used probe tastants that were novel to the session, and the current study used probe tastants that were pseudorandomly chosen from the existing stimulus set. This final point is of particular interest for interference-based accounts of primacy and recency.

When lists of information are being presented, interference is created in two ways: within-list and across-list. Within-list proactive interference occurs when stimuli from the same list distort each other's memory representations. When a list has high levels of within-list interference, participants best remember the final stimulus presented (i.e., recency) because no competing stimulus follows it. Across-list interference, then, occurs when stimuli from other lists distorts the memory of the current list's stimuli. More time between list presentations means a reduction in across-list interference, usually resulting in the first stimulus presented being best remembered (i.e., primacy). With a relatively small stimulus set – 4 in the case of Johnson et al. (2014) and 8 in the current study – proactive interference is likely to disrupt memory. Substantial across-list interference resulted from having a small stimulus set and relatively short delay times. In such cases, the final stimulus presented in a list is most easily correctly recognized because it has not received as much across-list and within-list interference as list positions 1 and 2. Thus, interference theory easily accounts for Experiment 2's data. If interference theory can describe the findings of taste list memory, it should also be able to make predictions about primacy and recency as well.

When Wright (1998) tested auditory list memory, proactive interference created within-list interference with small (8-item) stimulus sets. By increasing the amount of time before the probe, the recency effect disappeared and reversed to a primacy effect. Experiment 2.1 replicates Experiment 2 with one important difference: the delay before the recognition probe is presented has been doubled from 30 s to 60 s. By expanding the total time before the probe is presented, across list proactive interference should be disrupted, allowing for stimuli presented early in the list (i.e., list position 1) to be remembered better. In addition, with the extended delay within-list interference should be reduced as retroactive interference dissipates as the probe delay increases. Likewise within-list proactive interference increases with delay and would have a deleterious effect on the tastants at the end of a list. Together, the reduction in across-list proactive interference and the shift of within-list interference should increase recognition for tastants at the beginning of the list.

Additionally, a follow-up to Experiment 2 is warranted to ensure that effects of recency are not due to participants failing to discharge or rinse out their mouths during the probe delay. If the traces of the final tastant are still present in participants' mouths when the recognition probe is presented, it would allow for an easier discrimination. Johnson and Vickers (2004) show evidence that distilled water alone can neutralize traces of tastants, but this tastant-trace explanation would be hard to dispel without the demonstration of a primacy effect. The goal of Experiment 2.1, then, is to test for a primacy effect to address these concerns.

Experiment 2.1

The results of Experiment 2 show that participants were able to memorize lists of tastants over a delay. While a recency effect was found, there was no evidence for primacy. One potential explanation for this finding is that participants did not sufficiently rinse their mouths during the delay. This would allow trace amounts of the most recent tastant to linger in the mouth of participants, allowing for an easier discrimination during the probe phase of the trial. Thus, a primacy effect would help rule out this potential criticism. In order to test for a primacy effect, the delay between list and probe was expanded from a 30-s interval to a 60-s interval. Increasing the delay should shift patterns of interference, potentially diminishing the recency effect in favor of primacy (Santiago & Wright, 1984; Wright, 1998).

Experiment 2.1 Methods

20 participants were recruited from Auburn University's Sona system. Students that participated in either Experiment 1, Experiment 1.1, or Experiment 2 were not eligible for the study. Similar to previous experiments, participants were recruited for times between 9AM and 5PM with an hour taken off at noon to avoid any contributing effects of lunch. Ages ranged from 18 to 21 (M = 19.5 years), with 14 participants identifying as female, and 5 reporting that their left hand was their dominant hand. Total participation in this study lasted no longer than one hour.

All specifications of Experiment 2 were replicated with the exception that the delay was extended in length to 60 s.

Experiment 2.1 Results and Discussion

Participants were able to successfully discriminate between probe stimuli that did and did not appear in the sample list; recognition accuracy was significantly above chance (50%) as confirmed by a one-sample *t*-test, $t(19) = 6.28$, $p < .01$, $d = 2.88$. Participants performed above chance on both “same” and “different” trials, $t(19) > 3.79$, $p < .01$, $d = 1.74$, and accuracy between these trial types did not vary, according a paired-samples *t*-test, $t(19) = 0.07$, $p = .95$, $d = 0.03$.

Figure 16 shows the mean recognition accuracy across list position. To analyze the form of the serial-position function, the list position slopes were calculated for each participant and testes against 0. A one-sample *t*-test showed that the mean slope (-21.8%) for recognition accuracy decreased with list position, $t(19) = 3$, $p < .01$, $d = 1.38$. A one-way repeated measures ANOVA of List Position (1, 2, 3) found a main effect, F(2, 38) = 5.5, $p < .01$, $\eta_\rho^2 = .225$. Polynomial contrasts showed that accuracy held a significant, negatively linear relationship across list position, $F(1, 19) = 9.06$, $p < .01$, $\eta_\rho^2 = .323$. This downward slope was confirmed with Bonferroni-corrected pairwise comparison *t*-tests that show that accuracy was significantly higher on list position 1 compared to list position 3, $p < .01$. Accuracy did not differ between list positions 1 and 2 ($p = .06$) or list positions 2 and 3 ($p = .31$).

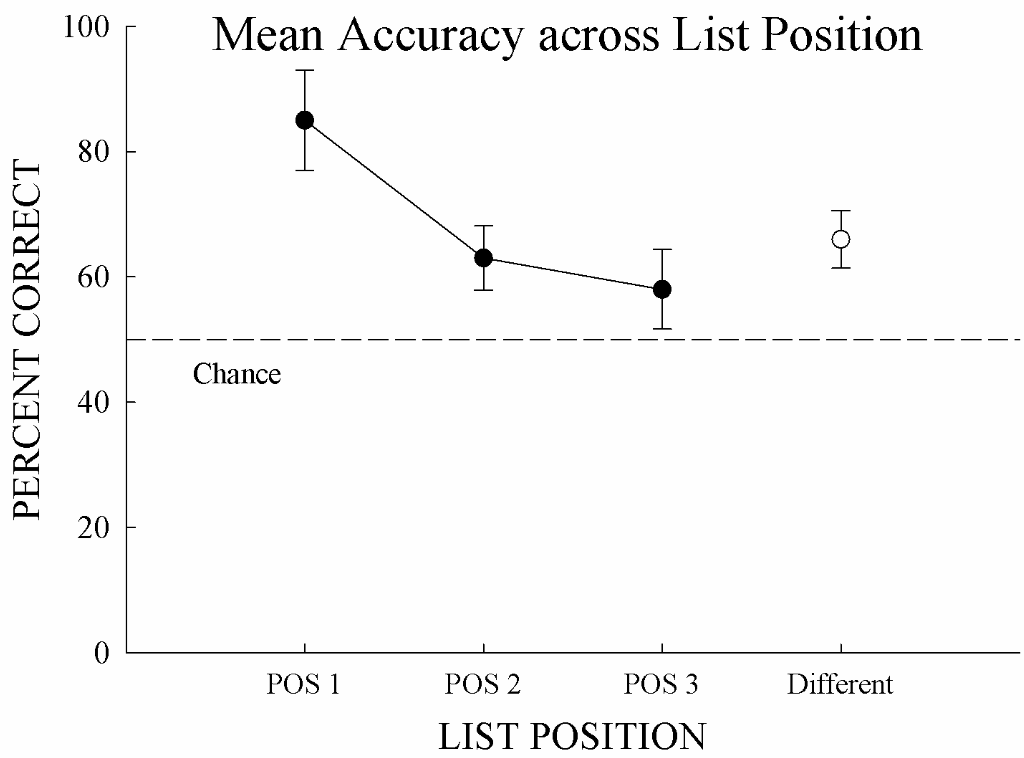

Figure 16. Mean percent correct for “same” trials (filled symbols) and “different” trials (open symbol). Participants demonstrated a primacy effect, with accuracy of “same” trials the highest with probes originally presented in list position 1. Chance is represented by the dashed line, and error bars represent the standard error of the mean.

General Discussion

Across four experiments, participants demonstrated the ability to remember tastes across delays and in the presence of concurrent taste-related information. To test for this taste-specific memory store, traditional memory procedures of DMTS and serial-probe recognition were used. The overarching goal of these experiments was to test for the presence of a short-term memory similar to that of vision and audition but for taste. Short-term memory for vision and audition is characterized by a sensory-specific, brief, high-resolution capacity that is sensitive to within-modality interference, and the main finding of this series of experiments is that such an analogous store for taste exists.

In Experiment 1, participants were required to memorize a sample tastant across a delay, compare this sample with a second tastant, and judge whether or not the two tastants were the same. This process required the ability to temporarily store a representation of taste. To ensure that participants were not simply storing verbal information representing taste, a verbal distractor task (articulatory suppression) was used during the delay. If tastes were unable to be stored across a delay, or if participants used verbal means to store this information, recognition accuracy would be no different from chance. Instead, participants performed above chance in recognition "same" and "different" probes. Further, participants' own ratings of stimulus intensity, pleasure, and verbalizability were model against accuracy, but these three variables held no predictive value. If participants perceive some stimuli to be more verbalizable than others, it did not benefit their recognition performance.

On the surface, the results of Experiment 1 are in direct contention with past research that memories of taste are unreliable (Barker & Weaver, 1983; Stevenson & Prescott, 1997; Vanne, Tuorila, & Laurinen, 1998). The difference between the current study and these previous investigations lies largely with what is being asked of the participant. Rather than asking participants if the probe stimulus is less, more, or equivalently intense as the sample, Experiment 1 had participants respond if the two stimuli were "same" or "different". Participants were specifically instructed that if the two stimuli were not identical in taste or intensity to respond "same". Experiment 1 also shows that initial judgments between two tastes are poor, with participants requiring a sort of calibration before being able to discrimination reliably well between taste. Participants showed a bias to report that these first two tastes were "different".

This initial bias is important in the light of past research, especially for taste experiments using first-trial data. Additionally, Experiment 1's stimuli varied along two distinct dimensions: taste and concentration. The perceptual distance between the within-taste discriminations (e.g., Highly Salty and Moderately Salty) was beyond the absolute threshold and JNDs as dictated in the literature (Bartoshuk, 1978).

The stimulus set used in Experiment 1 was not perfect, however, so Experiment 1.1 altered the perceptual distance between Moderately Bitter and Highly Bitter tastants. In Experiment 1, participants reliably judged Moderately Bitter and Highly Bitter to be the same tastant. This constituted a problem moving forward because bitter Within-Taste discriminations composed 25% of all Within-Taste trials. However, by diluting the Moderately Bitter tastant by 30%, participants were able to discriminate between the two tastants in DMTS. These participants replicated the effects of Experiment 1, but their recognition accuracy was above chance on Within-Taste trials. This contrasts with Experiment 1's participants, whose accuracy on the similar trials were equivalent to chance. The final two experiments used this improved stimulus set to examine list memory for tastes.

The results of Experiments 2 and 2.1 demonstrate serial-position effects for gustatory objects. Memory functions for list position order were created by testing participants with 3-item lists of tastants. At the 30-s delay, participants show a recency effect, with the final tastant of the list being recognized most easily. But at the 60-s delay, this effect shifts so that the first tastant of the list is most easily recognized, thus creating a primacy effect. Accuracy in Experiments 2 and 2.1 were compared in a two-way repeated-measures ANOVA of Delay (30 s, 60 s) and List Position (1, 2, 3). This ANOVA found no main effect of delay ($p = .9$), and no effect of list position ($p = .51$), but a significant interaction between the two factors, $F(2, 38) = 6.769$, $p < .01$.

This interaction was due to accuracy on list position 1 increasing 23.7% over the increased delay length, , $t(19) = 3.9$, $p < .01$, accuracy on list position 3 decreasing 21.2% over the increased delay, $t(19) = 2.27$, $p < .05$. These experiments not only show that participants can encode and store multiple tastants at once, but that this short-term memory is susceptible to the same recency to primacy shift found in visual list memory (Wright, 1998).

Implications for Working Memory Theory

The current set of studies offer evidence that gustatory objects can be stored and withheld within WM. But does this necessitate a separate, independent short-term memory store for taste? In an overview of serial-order and WM, Hurlstone, Hitch, and Baddeley (2014) outline three key arguments for separate visual and verbal short-term memory stores. The first of these arguments regards the presence of interference in dual-task studies. In a short-term memory task with verbal information, performance is not vulnerable to nonverbal interference. In other words, when participants are required to remember a list of words, spatial distractors affects behavior much less than a verbal distractors. In all of the experiments presented here, participants were able to reliably memorize tastants even when given a verbal distractor task. If taste memory was mediated by an episodic buffer, as Baddeley (2012) suggests, performance would have been disrupted by the introduction of articulatory suppression. If participants were using a verbal strategy, or if the articulatory suppression was ineffective, accuracy would likely have been close to perfect, as human verbal memory can easily store 1 – 3 words over a short delay. The other two arguments for fractionated short-term stores are neurological in nature and discussed below.

Neuroimaging data has provided a wealth of support for individual short-term stores based on the neural networks recruited by visuo-spatial and verbal memory (e.g., Smith & Jonides, 1997; Kelley et al., 1998; Owen, McMillan, Laird & Bullmore, 2005; Postle, 2006;

Daniel, Katz, & Robinson, under review). Brain activation is qualitatively different depending on whether participants are tasked with remembering words (verbal) or abstract polygons (nonverbal). Similarly, short-term memory stores have been discovered for touch (Harris et al., 2002) and olfaction (Zelano et al., 2009). The behavioral data reported here suggests that taste may be no different, and that a localized region of the brain is responsible for maintaining representations of gustatory objects. Should such an area exist, it would likely be found in the primary gustatory cortex. This area, if lesioned or ablated, can lead to gustatory agnosia (Kiefer & Orr, 1992; Small et al., 2005). The third and final reason Hurlstone et al. (2014) propose that vision and audition be thought of as separate, independent stores is related to agnosia. If one of these short-term memory stores can effectively be removed without serious detriment to the other, it's likely that they do not rely on each other for basic memory functions. The existence of gustatory agnosia supports the findings of the experiments reported in this paper.

Future Directions. These results offer more evidence that classic models of WM warrant further consideration and development. With the availability of neuroimaging technology, future models of WM should be able to account for data from both behavioral and neural domains. Moving forward, it is imperative to consider the integration of the less-studied touch, olfaction, taste, and their role in memory and attention.

Some of the foundation for taste WM is established, but several questions remain. Of particular interest is how this short-term store for tastants compares to that of the other senses. In what ways is taste WM similar to vision, audition, and smell, and in what ways is it unique? What is its capacity? How susceptible is it to interference? Does flavor enhance taste memory or distort it? And perhaps most importantly, does taste memory recruit its own unique neural network compared to vision, audition, and olfaction? The current experiments used DMTS and list memory to measure taste WM, but several similar procedures, such as N-back or dual-task, should be used to study taste as well. Doing so will fill a considerable gap in our knowledge of taste's role in memory.

Conclusion

Nearly a century of memory research has been devoted almost entirely to the study of words, numbers, and pictures. Using traditional memory procedures with an unconventional stimulus set, a new taste-relevant short-term memory store was detected. Contrary to the predictions made by the Baddeley (2000) model of WM, taste appears to have its own memory store, independent of verbal coding. With this discovery, it is important to consider the comparison of taste memory with other sensory domains. The current data serve as the first step in answering these questions, and in so doing, changing our theoretical understanding of human memory.

References

Andrade, J., & Donaldson, L. (2007). Evidence for an olfactory store in working memory. *Psychologia*, *50*, 76-89.

Atkinson, R. C., & Shiffrin, R. M. (1968). Human memory: A proposed system and its control processes. *Psychology of learning and motivation*, *2*, 89-195.

Baddeley, A. D., & Hitch, G. J. (1974). Working memory. *The psychology of learning and motivation*, *8*, 47-89.

Baddeley, A. (1992). Working memory. *Science*, *255*(5044), 556-559.

Baddeley, A. (1994). The magical number seven: still magic after all these years? *Psychological review*, *101*(2), 353-356. doi: 10.1037/0033-295X.101.2.353

Baddeley, A. D. (2000). The episodic buffer: a new component of working memory? *Trends in cognitive sciences*, *4*(11), 417–423.

Baddeley, A. (2012). Working memory: theories, models, and controversies. *Annual review of psychology*, *63*, 1-29.

Barker, L. M. (1982). Building memories for food. In L. M. Barker (Ed.) *The psychobiology of human food selection*. AVI Publishing Co. Inc..

Barker, L. M., & Weaver III, C. A. (1983). Rapid, permanent, loss of memory for absolute intensity of taste and smell. *Bulletin of the Psychonomic Society*, *21*(4), 281-284.

Bartoshuk, L. M. (1978). The psychophysics of taste. *The American Journal of Clinical Nutrition*, *31*(6), 1068-1077.

Breslin, P. A., & Spector, A. C. (2008). Mammalian taste perception. *Current Biology*, *18*(4), R148-R155.

Chaudhari, N., Landin, A. M., & Roper, S. D. (2000). A metabotropic glutamate receptor variant functions as a taste receptor. *Nature neuroscience*, *3*(2), 113-119.

Chandrashekar, J., Hoon, M. A., Ryba, N. J., & Zuker, C. S. (2006). The receptors and cells for mammalian taste. *Nature*, *444*(7117), 288-294.

Chandrashekar, J., Yarmolinsky, D., von Buchholtz, L., Oka, Y., Sly, W., Ryba, N. J., & Zuker, C. S. (2009). The taste of carbonation. *Science*, *326*(5951), 443-445.

Chen, X., Gabitto, M., Peng, Y., Ryba, N. J., & Zuker, C. S. (2011). A gustotopic map of taste qualities in the mammalian brain. *Science*,*333*(6047), 1262-1266.

Clarke, S., Bellmann, A., Meuli, R. A., Assal, G., & Steck, A. J. (2000). Auditory agnosia and auditory spatial deficits following left hemispheric lesions: evidence for distinct processing pathways. *Neuropsychologia*, *38*(6), 797-807.

Crowder, R. G. (1982). The demise of short-term memory. *Acta Psychologica*, *50*(3), 291-323.

Daniel, T. A., Katz, J. S., Robinson, J. L. (in press). Delayed match-to-sample in working memory: A BrainMap meta-analysis. *Brain and Behavior*.

Deese, J., & Kaufman, R. (1957). Serial effects in recall of unorganized and sequentially organized verbal material. *Journal of Experimental Psychology*, *54*(3), 180-187.

Drewnowski, A. (1997). Taste preferences and food intake. *Annual review of nutrition*, *17*(1), 237-253.

Ebbinghaus, H. (1913). *Memory: A contribution to experimental psychology* (No. 3). Teachers college, Columbia university.

Engen, T., & Ross, B. M. (1973). Long-term memory of odors with and without verbal descriptions. *Journal of experimental psychology*, *100*(2), 221.

Farah, M. J., Wilson, K. D., Maxwell Drain, H., & Tanaka, J. R. (1995). The inverted face inversion effect in prosopagnosia: Evidence for mandatory, face-specific perceptual mechanisms. *Vision research*, *35*(14), 2089-2093.

Farah, M. J. (2004). *Visual agnosia*. MIT press.

Faul, F., Erdfelder, E., Lang, A. G., & Buchner, A. (2007). G* Power 3: A flexible statistical power analysis program for the social, behavioral, and biomedical sciences. *Behavior research methods*, *39*(2), 175-191.

Gallace, A., & Spence, C. (2009). The cognitive and neural correlates of tactile memory. *Psychological bulletin*, *135*(3), 380.

Gaston, K. E. (1978). Brain mechanisms of conditioned taste aversion learning: A review of the literature. *Physiological Psychology*, *6*(3), 340-353.

Gelman, A., & Hill, J. (2006). *Data analysis using regression and multilevel/hierarchical models*. Cambridge University Press.

Gilson, E. Q., & Baddeley, A. D. (1969). Tactile short-term memory. *The Quarterly journal of experimental psychology*, *21*(2), 180-184.

Goldman-Rakic, P. S., Cools, A. R., & Srivastava, K. (1996). The prefrontal landscape: implications of functional architecture for understanding human mentation and the central executive [and Discussion]. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*,*351*(1346), 1445-1453.

Green, B. G., Nachtigal, D., Hammond, S., & Lim, J. (2012). Enhancement of retronasal odors by taste. *Chemical senses*, *37*(1), 77–86. doi:10.1093/chemse/bjr068

Hurlstone, M. J., Hitch, G. J., & Baddeley, A. D. (2014). Memory for serial order across domains: An overview of the literature and directions for future research. *Psychological bulletin*, *140*(2), 339.

Johnson, E. A., & Vickers, Z. (2004). The effectiveness of palate cleansing strategies for evaluating the bitterness of caffeine in cream cheese. *Food quality and preference*, *15*(4), 311-316.

Johnson, A. J., & Miles, C. (2009). Single-probe serial position recall: Evidence of modularity for olfactory, visual, and auditory short-term memory. *The quarterly journal of experimental psychology*, *62*(2), 267-275.

Johnson, A. J., Volp, A., & Miles, C. (2014). Immediate recognition memory for wine. *Journal of Cognitive Psychology*, *26*(2), 127-134.

Kelley, W. M., Miezin, F. M., McDermott, K. B., Buckner, R. L., Raichle, M. E., Cohen, N. J., ... & Petersen, S. E. (1998). Hemispheric specialization in human dorsal frontal cortex and medial temporal lobe for verbal and nonverbal memory encoding. *Neuron, 20*(5), 927-936.

Kiefer, S. W., Leach, L. R., & Braun, J. J. (1984). Taste agnosia following gustatory neocortex ablation: dissociation from odor and generality across taste qualities. *Behavioral neuroscience*, *98*(4), 590.

Kiefer, S. W., & Orr, M. R. (1992). Taste avoidance, but not aversion, learning in rats lacking gustatory cortex. *Behavioral neuroscience*, *106*(1), 140.

Köster, M. A., Prescott, J., & Köster, E. P. (2004). Incidental learning and memory for three basic tastes in food. *Chemical Senses*, *29*(5), 441-453.

Lawless, H., & Engen, T. (1977). Associations to odors: interference, mnemonics, and verbal labeling. *Journal of Experimental Psychology: Human Learning and Memory*, *3*(1), 52.

Li, X., Staszewski, L., Xu, H., Durick, K., Zoller, M., & Adler, E. (2002). Human receptors for sweet and umami taste. *Proceedings of the National Academy of Sciences*, *99*(7), 4692-4696.

Logie, R. H. (2011). The Functional Organization and Capacity Limits of Working Memory. *Current Directions in Psychological Science*, *20*(4), 240-245.

Manning, S. K. (1978). The effects of interpolated interference on tactual and visual short-term memory. *The American Journal of Psychology*, 445-459.

Mantonakis, A., Rodero, P., Lesschaeve, I., & Hastie, R. (2009). Order in choice effects of serial position on preferences. *Psychological Science*, *20*(11), 1309-1312.

McDonald, J. H. *Handbook of biological statistics* (3rd ed.). Sparky House Publishing, MD.

McNeil, J. E., & Warrington, E. K. (1993). Prosopagnosia: A face-specific disorder. *The Quarterly Journal of Experimental Psychology*, *46*(1), 1-10.

Mendez, M. F., & Ghajarnia, M. (2001). Agnosia for familiar faces and odors in a patient with right temporal lobe dysfunction. *Neurology*, *57*(3), 519-521.

Miller, G. A. (1956). The magical number seven, plus or minus two: some limits on our capacity for processing information. *Psychological review*,*63*(2), 81.

Morin-Audebrand, L., Mojet, J., Chabanet, C., Issanchou, S., Møller, P., Köster, E. P., & Sulmont-Rossé, C. (2012). The role of novelty detection in food memory. *Acta psychologica*, *139*(1), 233-238.

Moskowitz, H. R. (1972). Perceptual changes in taste mixtures. *Perception & Psychophysics*, *11*(4), 257-262.

Murdock, B. B. (1962). Direction of recall in short-term memory. Journal of Verbal Learning and Verbal Behavior, 1, 119-124.

Murphy, C., & Cain, W. S. (1980). Taste and olfaction: independence vs interaction. *Physiology & Behavior*, *24*(3), 601-605.

Nairne, J. S., & McNabb, W. L. (1985). More modality effects in the absence of sound. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *11*(3), 596.

Núñez-Jaramillo, L., Ramírez-Lugo, L., Herrera-Morales, W., & Miranda, M. I. (2010). Taste memory formation: latest advances and challenges.*Behavioural brain research*, *207*(2), 232-248.

Owen, A. M., McMillan, K. M., Laird, A. R., & Bullmore, E. (2005). N-back working memory paradigm: A meta-analysis of normative functional neuroimaging studies. *Human brain mapping*, *25*(1), 46-59.

Pashler, H. (1988). Familiarity and visual change detection. *Perception & Psychophysics*, *44*(4), 369–78.

Parr, W. V., Heatherbell, D., & White, K. G. (2002). Demystifying wine expertise: olfactory threshold, perceptual skill and semantic memory in expert and novice wine judges. *Chemical Senses*, *27*(8), 747-755.

Platz, T. (1996). Tactile agnosia Casuistic evidence and theoretical remarks on modality-specific meaning representations and sensorimotor integration. *Brain*, *119*(5), 1565-1574.

Postle, B. R. (2006). Working memory as an emergent property of the mind and brain. *Neuroscience*, *139*(1), 23-38.

R Core Team (2012). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN: 3-900051-07-00, URL http://www.R-project.org/.

Reed, C. L., Caselli, R. J., & Farah, M. J. (1996). Tactile agnosia underlying impairment and implications for normal tactile object recognition. *Brain*,*119*(3), 875-888.

Reed, P., Croft, H., & Yeomans, M. (1996). Rats' memory for serially presented novel flavours: Evidence for non-spatial primacy effects. *The Quarterly Journal of Experimental Psychology: Section B*, *49*(2), 174-187.

Rottschy, C., Langner, R., Dogan, I., Reetz, K., Laird, A. R., Schulz, J. B., ... & Eickhoff, S. B. (2012). Modelling neural correlates of working memory: a coordinate-based meta-analysis. *Neuroimage*, *60*(1), 830-846.

Rozin, P. (1982). “Taste-smell confusions” and the duality of the olfactory sense. *Perception & Psychophysics*, 31(4), 397–401.

Sands, S. F., & Wright, A. A. (1980). Serial probe recognition performance by a rhesus monkey and a human with 10-and 20-item lists. *Journal of Experimental Psychology: Animal Behavior Processes*, *6*(4), 386.

Santiago, H. C., & Wright, A. A. (1984). Pigeon memory: Same/different concept learning, serial probe recognition acquisition, and probe delay effects on the serial-position function. *Journal of Experimental Psychology: Animal Behavior Processes*, *10*(4), 498.

Small, D. M., Bernasconi, N., Bernasconi, A., Sziklas, V., & Jones-Gotman, M. (2005). Gustatory agnosia. *Neurology*, *64*(2), 311-317.

Smith, E. E., & Jonides, J. (1997). Working memory: A view from neuroimaging. *Cognitive psychology*, *33*(1), 5-42.

Spence, C. (2011). Cross-modal correspondences: a tutorial review. *Attention, perception & psychophysics*, *73*(4), 971–95. doi:10.3758/s13414-010-0073-7

Stevenson, R. J., & Prescott, J. (1997). Judgments of chemosensory mixtures in memory. *Acta psychologica*, *95*(2), 195-214.

Stevenson, R. J., Prescott, J., & Boakes, R. a. (1999). Confusing tastes and smells: how odours can influence the perception of sweet and sour tastes. *Chemical Senses*, *24*(6), 627–35.

Valentin, D., Chollet, S., Beal, S., & Patris, B. (2007). Expertise and memory for beers and beer olfactory compounds. *Food quality and preference*,*18*(5), 776-785.

Vanne, M., Tuorila, H., & Laurinen, P. (1998). Recalling sweet taste intensities in the presence and absence of other tastes. *Chemical senses*,*23*(3), 295-301.

Veldhuizen, M. G., Albrecht, J., Zelano, C., Boesveldt, S., Breslin, P., & Lundström, J. N. (2011). Identification of human gustatory cortex by activation likelihood estimation. *Human brain mapping*, *32*(12), 2256-2266.

Verendeev, A., & Riley, A. L. (2012). Conditioned taste aversion and drugs of abuse: History and interpretation. *Neuroscience & Biobehavioral Reviews*,*36*(10), 2193-2205.

Ward, G., Avons, S. E., & Mellings, L. (2005). Serial position in curves in short-term memory: Functional equivalence across modalities. *Memory*, *13*, 308-317.

Watkins, M. J., & Watkins, O. C. (1974). A tactile suffix effect. *Memory & Cognition*, *2*(1), 176-180.

Warton, D. I., & Hui, F. K. (2011). The arcsine is asinine: the analysis of proportions in ecology. *Ecology*, *92*(1), 3-10.

White, T. L., & Treisman, M. (1997). A comparison of the encoding of content and order in olfactory memory and in memory for visually presented verbal materials. *British Journal of Psychology*, *88*(3), 459-472.

White, T. L. (1998). Olfactory memory: the long and short of it. *Chemical senses*, *23*(4), 433-441.

Wickens, C. D. (1991). Processing resources and attention. In D. L. Damos (Ed.), *Multiple-task performance*, 3-34. Bristol: Tailer & Francis, Ltd.

Wright, A., Santiago, H., Sands, S., Kendrick, D., & Cook, R. (1985). Memory processing of serial lists by pigeons, monkeys, and people. *Science* 229 (4710), 287-289.

Wright, A. A., Cook, R. G., Rivera, J. J., Shyan, M. R., Neiworth, J. J., & Jitsumori, M. (1990). Naming, rehearsal, and interstimulus interval effects in memory processing. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *16*(6), 1043.

Wright, A. A. (1998). Auditory and visual serial position functions obey different laws. *Psychonomic Bulletin & Review*, *5*(4), 564-584.

Wright, A. A., & Roediger, H. L. (2003). Interference processes in monkey auditory list memory. *Psychonomic bulletin & review*, *10*(3), 696-702.

Zelano, C., Montag, J., Khan, R., & Sobel, N. (2009). A specialized odor memory buffer in primary olfactory cortex. *PloS one*, *4*(3), e4965. doi:10.1371/journal.pone.0004965

Appendix A

All participants, prior to the beginning of the memory task, were given the following questions to answer:

What gender do you identify with?

What is your age in years?

Are you right-handed or left-handed?

Do you have any food allergies at all?

When was the last time you had something to eat or drink?

How many cups of coffee do you drink daily?

How many cans of soda do you drink daily?

Do you smoke regularly?

Appendix B

Regardless of your responses in the following survey, you will receive full credit for your participation in this study. Please answer the below questions to the best of your ability.

1) Did you ever feel bored in this task?

2) Did you ever find yourself unable to pay attention during this task?

3) Did you feel too full at the end of the experiment?

4) Was there any particular strategy that you used to remember the tastes?

5) During the delay, what did you think about before you were given the second taste?