The Capacity and Organization of Gustatory Working Memory

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Abstract

Remembering a particular taste is crucial in food intake and associative learning. We investigated whether taste can be dynamically encoded, maintained, and retrieved on short time-scales consistent with working memory (WM). We used novel single and multi-item taste recognition tasks to investigate the organization and capacity of gustatory WM. In Experiment 1, we show that a single taste can be reliably recognized despite multiple oro-sensory interferences suggesting active and resilient maintenance. When multiple tastes were presented, the resolution with which these could be maintained, depended on their serial position implying a role of attention. Participants reliably recognized up to three tastes, compatible with a limited capacity of gustatory WM. Lastly, recognition was better for match than foil trials likely due to increased stimulus similarity in foil trials. Together, the results advocate a hybrid model of gustatory WM with a limited number of slots where items are stored with varying precision.

Introduction

Working memory (WM) is the faculty of actively storing information for short periods[1,2]. Since its original formulation, the organization of WM and its neural substrate has been subject to extensive investigation[3–7]. However, research into the generality of WM for different kinds of information[8–10] has largely neglected an important chemical sense: the sense of taste. This neglect is surprising given the relevance of taste information processing to identify nutrients and avoid toxins and with that, maintain homeostatic balance[11,12]. Furthermore, the taste of previously consumed food substances guides future dietary decisions. As this memory for prior tastes is essential for adaptive behavior, long-term gustatory memory, particularly conditioned taste-aversion, has been the focus of various studies[13–18]. However, the possibility that multiple recently encountered tastes such as sweet or sour could be discretely stored and maintained in WM has received almost no consideration (see Daniel & Katz[19] for an exception). Consequently, whether and to what extent information about multiple tastes can be actively maintained in WM and its storage organization remain elusive.

In other sensory modalities, the study of WM's storage capacity has provided valuable insights into its organization - for example, as distributed resource-based[20,21] or fixed slot-based[22,23]. Here, we adopted a similar strategy. Due to the methodological challenges of delivering multiple taste stimuli in a precisely controlled sequential manner (see Methods), we operationalized gustatory WM’s storage capacity as the maximum number of unique tastes (i.e., items) that could be discretely maintained to enable subsequent recognition. However, relating such a capacity limit to WM organization is challenging due to several considerations specific to the gustatory system’s, mostly peripheral organization.

A general view of a limited WM capacity is that it explains why recognition accuracy decreases with increasing set size[2,24–26] (Fig. 1a). However, such decreases in recognition accuracy can be influenced by peripheral factors unrelated to WM, such as the irrelevant multisensory information that accompanies many sensory experiences. This constitutes a particular concern for gustation, which is inherently coupled with non-gustatory sensations. For instance, when eating an apple, its appearance, smell, texture, temperature, even the sound when we take a bite are inextricably linked with its taste[27–29]. These factors can have complex direct and indirect effects on the recognition processes and distort capacity estimates of taste WM. To limit alternate information channels due to crossmodal cues, all stimuli in our study were odorless and colorless liquids with similar viscosity presented at a constant temperature. However, tastes are unavoidably associated with oro-somatosensory touch stimulation due to contact with the tongue and mouth. These stimulations might conceivably act as attentional “disturbances” that might degrade WM performance, given attention’s prominent role in WM [9,30–32].

Additionally, the possible mixing of residuals with subsequent tastants on the tongue as well as the relative proneness of the gustatory system to quick sensory adaptation[33–35] are potential sources of sensory interference that might reduce the fidelity with which tastes are encoded in WM. This concern was countered with a rinse between stimuli that removed residual tastes.

Stimulus-similarity effects[36] are also an important consideration. To examine their possible role, we used simple tastes and binary mixtures. The mixtures expanded the gustatory stimulus space beyond a few basic tastes. The additional features in mixtures compared to simple tastes could take up more memory and affect performance if a feature-based organization of WM is assumed, which is, notably, debated in the visual domain (Luck & Vogel[22], but see Oberauer & Eichenberger[37]). We assumed that stimulus complexity would have only a minor effect, if any, because the fast pace and high task-demands in our study made it very unlikely that participants used an analytic strategy to identify the mixture's components, which was confirmed by informal reports of our participants. If it had an effect, it would be an underestimation of the WM’s capacity in our study, in line with observations in visual WM[38].

Based on these considerations, in the present study, we investigated the organization of gustatory WM in two experiments. To obtain a baseline measure of the magnitude of critical non-capacity related factors, i.e. sensory interference and attentional distraction, in Experiment 1, we evaluated recognition of a single taste item in the presence of a variable number of oro-sensory disturbances between the item and the probe. The opposing hypothesized effects of sensory and attentional interference (see Fig. 1b, Methods) permit us to assess their contribution to gustatory WM, as sensory interference would be hypothesized to increase taste recognition accuracy with time. In contrast,attentional disturbance would be hypothesized to cause a marked drop. In Experiment 2, we used a list memory task where participants were to remember a set of distinct sequentially presented tastes of different set sizes to obtain a first estimate of the gustatory WM's unknown capacity.

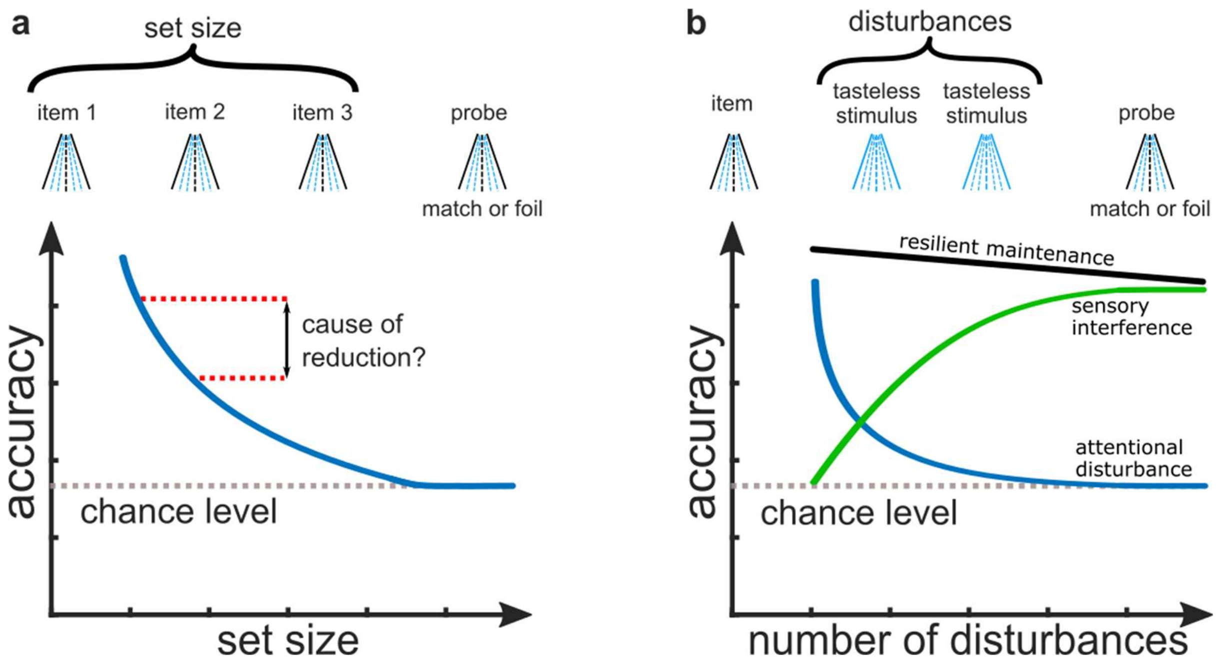

Fig. 1 | Illustration of hypothetical outcomes and inference effects in estimating taste WM capacity. a, A multi-item recognition task (upper row) requires a judgment whether the probe taste corresponds to one of the previously encountered taste items (match) or not (foil). The lower panel illustrates the typically expected accuracy decrease with increasing set size. **b**, In a single-item recognition task, a set consists of a single item with following items replaced by tasteless stimuli (disturbances). The lower panel illustrates predicted accuracy changes with an increasing number of disturbances based on alternative hypothesized mechanisms. *Sensory interference* predicts an increase in accuracy with increasing disturbances and time. *Attentional disturbance* predicts a steep decrease in accuracy with increasing disturbances and time. *Resilient maintenance* predicts accuracy that is relatively unaffected by disturbances and time.

Results

Stimulus validation

Stimuli were ten different tastes and a tasteless artificial saliva solution (see Methods: Stimuli and Apparatus). Due to the large inter-individual variability in taste perception[39–42], validating that participants tasted the stimuli was critical. Before both experiments, we used a taste detection and evaluation task to test whether participants could perceive the tastants. For this, participants were presented the taste and tasteless stimuli in a randomized order. The subjects were asked to indicate whether they tasted something or not by button press and the detected tastes were further rated about intensity and pleasantness. Taste detection accuracy was high in both experiments (Experiment 1: M = 97.5%, SD = 6%; Experiment 2: M = 98.5%, SD = 4%; Suppl. Fig. 1a). Of the ten tastes, bitter had the lowest detection accuracy (Experiment 1: M = 87%; Experiment 2: M = 88.8%), consistent with the known variability in bitter taste perception[41]. All tastes were rated as intermediately intense (Experiment 1: M=6.52, SD=1.61; Experiment 2: M=6.74, SD=1.42; Suppl. Fig. 1b) and moderately pleasant (Experiment 1: M=4.58, SD=1.51, Experiment 2: M=4.50, SD= 1.49l; Suppl. Fig. 1c). The high consistency in taste detection accuracy and ratings of intensity and pleasantness in the two experiments demonstrated that the stimuli were reliably perceived across participants.

Single-item taste recognition task (Experiment 1)

First, we explored the primary conditions that characterize gustatory WM: resilient representations, awareness of performance, and stimulus-similarity effects. We used a single taste memory to non-taste disturbances using a single-item taste recognition (SIR) task (Fig. 1b; see Methods). Each trial began with the presentation of a single taste item that participants had to remember. This taste item was followed by tasteless stimuli that simulated the task-irrelevant oro-sensory disturbances that accompany a true taste presentation. The trial ended with the presentation of a second tastant (probe). Participants indicated whether the probe was identical to (match) or different from (foil) the first taste item followed by a rating of their confidence in this decision. To limit expectancy effects, the number of disturbances on each trial was unknown to participants and, on a fraction of trials, the probe was presented directly after the item without intervening disturbance stimuli. If the item was resiliently maintained, recognition accuracy should be similar across the numbers of disturbances. In contrast, if the item's representation was affected by attentional distraction or sensory interference, accuracy should markedly change with an increasing number of oro-sensory disturbances (Fig. 1b).

Recognition accuracy was well above chance at all levels of disturbance (Fig. 2a). The accuracy was highest on trials with a single disturbance and exhibited only small decrements with each additional disturbance (repeated measures analysis of variance, rmANOVA: $F_{4,80}=6.25$, $p<0.001$, $\eta_p^2=0.23$). Relative to trials with one disturbance (M=82%, SD=6.38%), the accuracy was reduced by only 2% on trials with two disturbances (M=80%, SD=5.22%; $t_{20}=1.56$, $d=0.34$, $p_{bonf}=1$, 95% CI=[-0.019, 0.056]), by 5% on trials with three disturbances (M=77%, SD=5.78%; $t_{20}=4.15$, $d=0.91$, $p_{bonf}=0.005$, 95% CI=[0.013, 0.091]), and by 6% on trials with four disturbances (M=76%, SD=6.6%; $t_{20}=3.61$, $d=0.79$, $p_{bonf} = 0.017$, 95% CI=[0.008, 0.120]). Accuracy was lower when the probe was presented immediately after the taste than when presented after a single disturbance (M= 78%, SD= 7.70%; $t_{20}=-3.25$, $d=-0.71$, $p_{bonf}=0.04$; see Suppl. Table 1 for all pairwise comparisons). In summary, the relatively small decrements in recognition accuracy with increasing disturbances cannot be accounted for solely by either (i) attentional distraction/interference or (ii) sensory interference in gustatory WM (Fig. 1b). However, the lowered accuracy for zero disturbances suggests sensory interference in encoding the probe stimulus caused by the temporal proximity of the item and probe. We, therefore, restricted our subsequent analyses to disturbances ≥ 1.

To assess whether participants were aware of their performance, we assessed the link between confidence and accuracy. Confidence about recognition decisions had a strong veridical relationship to the accuracy of those decisions, i.e. trials with a higher confidence rating also had a higher accuracy (Fig. 2e; $F_{3,60}$=60.86, p<0.001, η_p^2=0.75) indicating that participants indeed monitored their performance.

We next tested whether the apparent resilience of taste recognition was indeed due to gustatory WM. For this, we exploited the well-known role of stimulus similarity in recognition with other stimulus modalities[43–47]. A comparable prediction here would be that recognition judgments that involve a WM for taste should depend on the chemical similarity of the item-probe pairs (see Daniel & Katz[19] for a similar argument). To test this, we compared the recognition accuracy for item-probe foil pairs that shared a chemical component (e.g., item: *sour*, probe: *sour-sweet*) with pairs that did not (e.g., item: *sour*, probe: *bitter*). Item-probe foil pairs with a shared component were assumed to be more similar (intermediate similar) than the pairs without a shared component (lowest in similarity). If this assumption holds, item-probe foil pairs of intermediate similarity should have a higher proportion of "same" responses (i.e., lower accuracy) than the pairs with the lowest similarity. By this rationale, the probability of "same" responses should be the highest for item-probe match pairs, which are chemically identical and hence perceptually highest in similarity.

In line with these predictions, the proportion of "same" responses varied between item-probe pairs (Fig. 2c; rmANOVA; $F_{2,40}$=516.51, p<0.001, η_p^2=0.9267) such that the proportion of "same" responses was highest for the item-probe match pairs that were highest in similarity (M=80.38%, SD=9.22%; highest similarity versus intermediate in similarity similar: t_{20}=20.16, p_{bonf}<0.001, d=4.4, 95% CI=[0.4017, 0.5213]; intermediate in similarity versus low in similarity: t_{20}=32.23, p_{bonf}<0.001, d=7.03, 95% CI=[0.6315, 0.7429]). Importantly, the proportion of "same" responses for the intermediary similar pairs (M=34.23%%, SD=11.84%) was significantly greater than for the lowest in similarity pairs (M=11.66%, SD=6.96%; t_{20}=10.68, p_{bonf}<0.001, d=2.33, 95% CI=[0.1704, 0.2809]).

The finding of a stimulus-similarity effect provided a way to evaluate why accuracy might reduce with increasing disturbances. Stimulus-similarity suggests that the combination of increasing disturbances and time-dependent forgetting might lower the precision of taste representations in memory. If so, this loss of precision should reduce the item-probe similarity (and accuracy) to a greater extent on match than foil trials. We hence focused our analyses on the comparison of match and foil trials.

As predicted, recognition accuracy on match and foil trials (Fig. 2d) were modulated differently by the number of disturbances (rmANOVA; Disturbances {1, 2, 3, 4} x Trial type {match, foil}; Disturbances*Type: $F_{3,60}$=6.70, p<0.001, η_p^2=0.26; Disturbances: $F_{3,60}$=8.33, p<0.001, η_p^2=0.29; Trial type: $F_{1,20}$=0.8511, p=0.3672, η_p^2= 0.04). While match trials showed an accuracy reduction of 13% with increasing disturbances ($F_{3,60}$=17.72, p<0.001), accuracy on foil trials was not measurably affected by the number of disturbances ($F_{3,60}$=0.31, p=0.82).

Additionally, response times (RTs; Fig. 2e) increased with the number of disturbances on match ($F_{3,60}$=11.32, p<0.001; see Suppl. Table 2a) but not foil ($F_{3,60}$=1.63, p=0.1923; see Suppl. Table 2b) trials. This resulted in a significant interaction (rmANOVA; Number of disturbances {1,2,3,4} x Trial type {match, foil}, Disturbances*Type: $F_{3,60}$=4.64, p<0.006, η_p^2=0.19; Disturbances: $F_{3,60}$=7.99, p<0.001, η_p^2=0.29; Type; $F_{1,20}$=3.19, p=0.089, η_p^2=0.14).

Furthermore, confidence was significantly lower for match than foil trials (Fig. 2f; rmANOVA; Disturbances {1,2,3,4} x Trial Type {match, foil}; Disturbances*Type: $F_{3,60}$=4.46, p=0.0068, η_p^2=0.18; Disturbances: $F_{3,60}$=10.45, p<0.001, η_p^2=0.34; Trial Type: $F_{1,20}$=30.97, p<0.001, η_p^2=0.61). The observed pattern of results where match trials were characterized by lower accuracy, higher RTs, and lower confidence than foil trials could be explained by stimulus similarity effects.

Consistent with the notion of a resilient taste WM representation, we found that cross-modal disturbances only had a minor influence on recognition accuracy, while the stimulus-similarity of item-probe pairs strongly affected recognition accuracy.

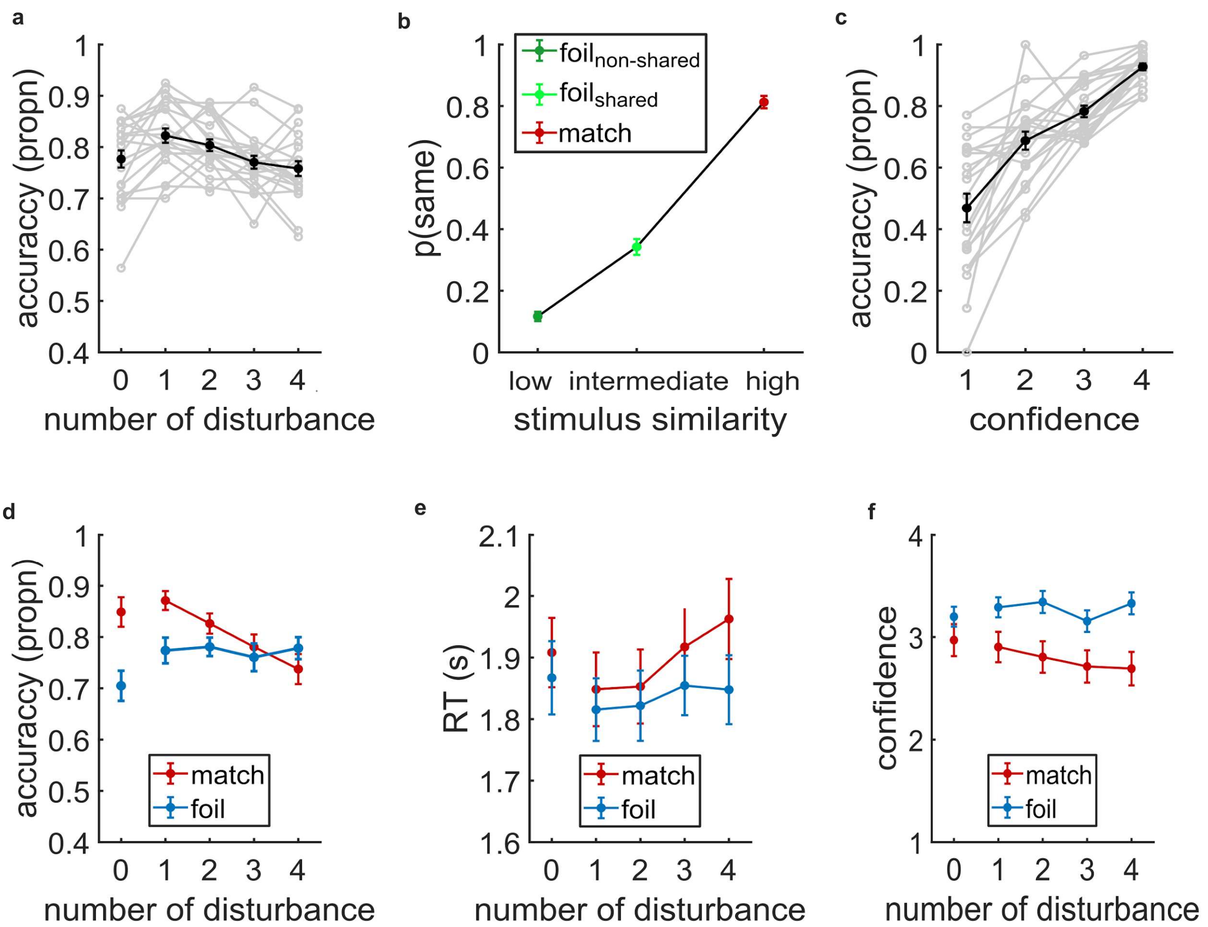

Fig. 2 | Experiment 1. a, Recognition memory accuracy (proportion correct, propn) across number of disturbances. **b**, Proportion of same responses for item-probe pairs with different levels of stimulus similarity: highest in similarity (match), intermediate in similarity (foil pairs, shared component), lowest in similarity (foil pairs, non-shared component). **c**, Accuracy for each confidence rating (1=not confident, 4=very confident). **d**, Recognition memory accuracy for match and foil trials across the number of disturbances. **e**, RT (in seconds) averaged across the number of disturbances, separately for match and foil trials. **f**, Confidence averaged across the number of disturbances, separately for match and foil trials. Data points are means, error bars are SEM. Gray lines represent single-subject data (N=21).

Multi-item taste recognition task (Experiment 2)

We next sought to estimate the capacity of taste working memory during a multi-item recognition (MIR) task (Fig. 1a; see Methods). Participants were to remember one to five sequentially presented tastes (items) on each trial, representing set sizes of one to five (referred to as S1 to S5). To minimize sensory interference, each item was followed by a tasteless rinse to cleanse sapid residues with minimal taste recognition disturbance (see Experiment 1). The memory for the item(s) was then tested with a probe stimulus. Participants indicated whether the probe matched any of the items in the remembered set (i.e., match) or not (i.e., foil) and then rated their confidence in that decision. We sought to assess WM capacity based on how recognition accuracy changed with increasing set size.

Recognition accuracy decreased monotonically with increasing set size (rmANOVA: $F_{4,76}=37.52$, $p<0.001$, $\eta_p^2=0.66$; Fig. 3a). Accuracy was highest for S1 (M=73.2%, SD=10.8%). Although each additional increase in set size lowered accuracy, the relative decrements in accuracy for each additional item was not uniform. The decrement was 8.9% for S2 relative to S1 ($t_{20}=4.93$, $d=1.10$, $p_{bonf}<0.001$, 95% CI=[0.023, 0.108]) and 7.9% for S3 relative to S2 ($t_{20}=3.71$, $d=0.83$, $p_{bonf}=0.015$, 95% CI=[0.008, 0.098]). However, each additional increase in set size beyond three produced smaller decrements, namely, 3.1% for S4 relative to S3 ($t_{20}=1.41$, $d=0.32$, $p_{bonf}=1$, 95% CI=[-0.024, 0.063]) and 5.4% for S5 relative to S4 ($t_{20}=2.13$, $d=0.48$, $p_{bonf}=0.469$, 95% CI=[-0.016, 0.089]; see Suppl. Table 3 for full pairwise comparisons). This is further supported by the qualitatively steeper negative slope fitting S1, S2, and S3 (Fig. 3a; -0.059) compared to the slope fitting S3, S4, and S5 (Fig. 3a; -0.026).

In the single-item recognition task (Experiment 1), recognition for similar item-probe foil pairs was lower than for dissimilar pairs. This stimulus-similarity effect on recognition reflects the representation of items rather than constraints on the number of items that can be remembered (i.e., capacity). Therefore, accounting for the role of stimulus-similarity with the multi-item sets was crucial to assess capacity. For the multi-item sets, the probability that a probe stimulus would share a taste-component with one or more items increased with set size. This could lead to increased errors on foil trials with increasing set size and, conversely, inflate the accuracy of match trials. Consistent with these hypothesized effects, trial type was a significant modulator of how recognition accuracy changed with set size (Fig. 3b; rmANOVA: Type {match, foil} x Set size {1,2,3,4,5}, Type*Set size: $F_{4,76}=4.19$, $p=0.027$, $\eta_p^2=0.18$; Type: $F_{1,19}=9.58$, $p=0.006$, $\eta_p^2=0.34$; Set size: $F_{4,76}=37.99$, $p<0.001$, $\eta_p^2=0.67$). Accuracy on foil trials decreased by 35.9% with a set size increase from one to five ($F_{4,76}=25.72$, $p<0.001$).The corresponding effect of set size on match trial accuracy was only 10.8% and not statistically significant ($F_{4,76}=2.21$, $p=0.08$).

We focused on match trials despite their potentially inflated accuracy with increasing set size to disentangle capacity constraints from the effects of stimulus-similarity. Although an accuracy reduction with increasing set size might be expected with capacity constraints, it was unclear whether these hypothesized capacity constraints had an ensemble effect that influenced all items of the set or whether it affected certain items more than others[20,21,25]. For example, all items in the set might be recognized with similar accuracy but this overall accuracy might reduce with increasing set size[21]. Alternatively, particular items might be recognized with higher accuracy while other items might be lost from memory due to capacity constraints (see Zhang & Luck[23]).

Fig. 3c shows the recognition accuracy for items at different serial positions in each set relative to the probe's timing on match trials. Inconsistent with an ensemble effect, for each set size, recognition accuracy across serial positions varied significantly (one-way rmANOVA; S_2: $F_{1,19}$=28.52, p_{bonf}<0.001, η_p^2=0.60; S_3: $F_{2,38}$=15.76, p<0.001, η_p^2=0.45; S_4: $F_{3,57}$=10.72, p<0.001, η_p^2=0.36; S_5: $F_{4,76}$=9.72, p<0.001, η_p^2=0.34). Consistent with a recency effect and incompatible with sensory adaptation, accuracy was highest for the last item in all set sizes; it decreased as the latency between the item and probe increased. Also, a primacy effect was only evident for set sizes 2 and 3. To assess whether all individual items were held in memory, we tested accuracy at each serial position against chance (50%). While most items showed above-chance accuracy, item 3 (abbreviated as I3) in S4 as well as I2 and I3 in S5 were not significantly different from chance (Suppl. Table 4). These results clearly show that a maximum of only three items could be successfully retained even when the set size required more than items to be remembered.

Mirroring its effects on accuracy, trial type also modulated how mean RTs on correct trials changed with set size (Fig. 4a; rmANOVA; Type {match, foil} x Set size {1,2,3,4,5}; Set size*Type: $F_{4,76}$=5.47, p=0.003, η_p^2=0.22; Type: $F_{1,19}$=7.76, p=0.012, η_p^2=0.29; Set size: $F_{4,76}$=1.16, p=0.326, η_p^2=0.06;). Foil RTs increased with set size by as much as 136.7ms from set size one to five (F_4=4.03, p=0.005) while the corresponding change in match RTs was not statistically significant (F_4=1.39, p=0.25).

Finally, we asked participants to rate their confidence about their response. As in Experiment 1, trials with a higher confidence rating also had a higher accuracy in Experiment 2 (Fig. 4b; rmANOVA; $F_{4,46}$=6.95, p=0.004, η_p^2=0.27). However, when separated by trial type (i.e., match and foil), confidence on correct trials changed with set size (Fig. 4c; rmANOVA; Type {match, foil} x Set size {1,2,3,4,5}; Type*Set size: $F_{4,76}$=12.85, p<0.001, η_p^2=0.404; Type: $F_{1,19}$=0.09, p=0.766, η_p^2=0.005; Set size: $F_{4,76}$=24.667, p<0.001, η_p^2=0.565). Resolving the interaction via simple main effects analyses, we found a reduction in confidence with increasing set-size for foil ($F_{4,76}$=29.44, p<0.001; see Suppl. Table 5b for pairwise tests) but not for match trials despite a significant simple main effect ($F_{4,76}$=5.07, p=0.001, Suppl. Table 5a). These findings suggest that confidence ratings might be an indicator of the subjective uncertainty arising from stimulus-similarity but not about capacity per se.

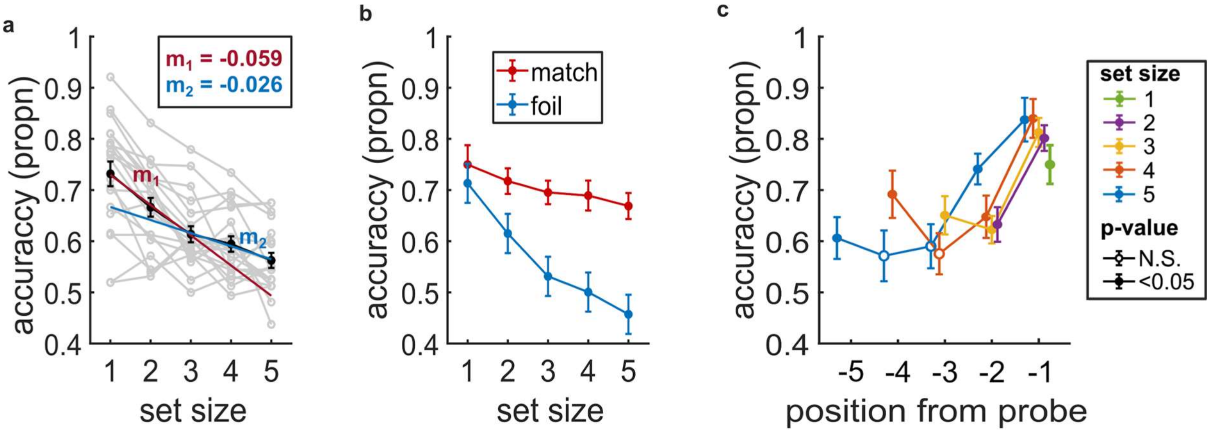

Fig. 3 | Recognition accuracy in Experiment 2. a, Recognition accuracy across set sizes. The red line is fitted to the first three data points with a slope (m_1) of -0.059 and the blue line is fitted to the last three data points with a slope (m_2) of -0.028. **b**, Recognition accuracy of match and foil trials across set size. **c,** Serial positions for match trials. Recognition accuracy for each item in a given set size relative to the probe. i.e, in set size 5, the first item presented is at position -5 from the probe. Accuracy is the proportion of correct responses (propn). Data points are means, error bars are SEM. Gray lines represent single-subject data (N=20). Filled circles represent accuracy significantly above chance (p<0.05); open circles represent accuracy not significantly above-chance.

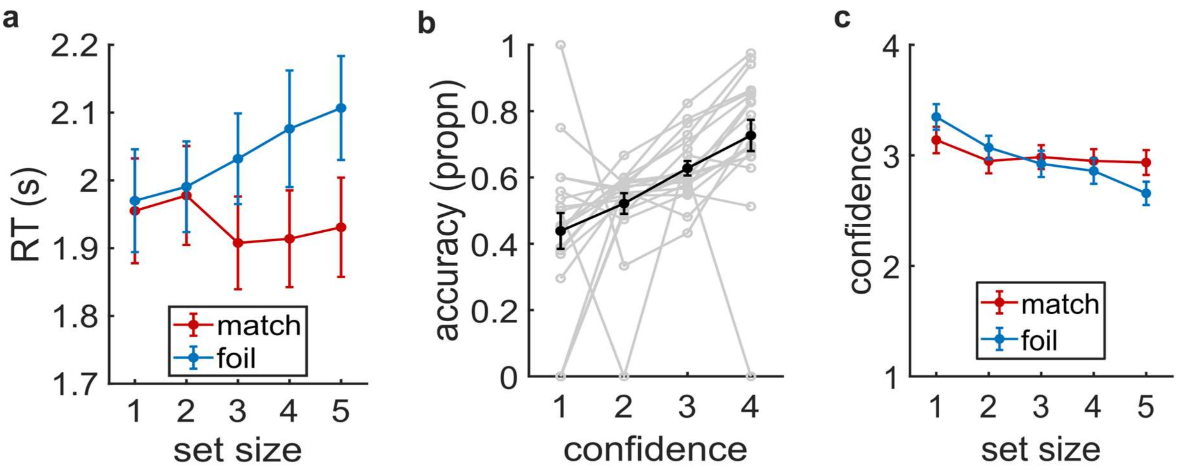

Fig. 4 | Reaction times and confidences in Experiment 2, **a,** Reaction times (in seconds) for match and foil trials across the set size. **b**, Recognition accuracy (in proportion correct) for each confidence level (1=not confident, 4=very confidence). **c**, Confidence for match and foil trials across the set size. Data points are means; error bars are SEM. Gray lines represent single-subject data (N=20).

Discussion

We used two novel single and multi item taste recognition tasks to investigate the organization and capacity limit of gustatory WM. We observed that the concept of WM extends to perceptual information from the gustatory system. Participants reliably recalled single items in the presence of oro-sensory distractions suggesting that tastes were actively and resiliently maintained. When multiple tastes were presented, participants distinctly and reliably maintained up to three tastes for subsequent recognition.

Resilient representation of single taste items

WM capacity requires attention[2], which can be exhausted by different aspects of the task - unrelated to WM. In contrast to a previous study, where participants were to grasp a cup, sip, and then spit out the stimuli[19], we used an automated taste delivery system to avoid the detrimental effects on WM performance of such multiple tasks[48]. Nevertheless, the orosensory disturbances could influence attention and WM maintenance. However, we found recognition accuracy for a single taste to be well above chance and only marginally influenced by the presentation of tasteless oro-sensory disturbances (Experiment 1). Although recognition accuracy decreased with each additional disturbance, and hence also with increasing time, these decrements were relatively small (2-6%), suggesting that attentional interference, if present, and time-based forgetting played only minor roles. It is, however, possible that the oro-sensory disturbances were ineffective at capturing attention. This interpretation is improbable though because the mere presentation of a tasteless liquid has been previously shown to capture attention[49], partly because stimulation by a tasteless liquid on the tongue can act as a taste cue since it elicits the same tactile sensation as a taste would.

Sensory interference from sensory adaptation as well as residues of prior stimuli could have impeded the encoding of subsequent stimuli[33–35,50–52], which would result in low recognition accuracy independent of memory, particularly for short item-probe intervals. Our results do not indicate adaptation or interference from taste residuals, both of which should increase recognition accuracy with increasing numbers of disturbances and time between item and probe as their detrimental effects fade. Although we cannot unequivocally exclude that (cross)adaptation took place, its effects were ineffectual such that tastes were suitably encoded and maintained to permit later retrieval. The higher recognition accuracy for item-probe pairs separated by a tasteless stimulus, compared to pairs that were not, indicates the absence of sensory interference, probably because residuals of the item were removed before probe presentation. We thus presented a tasteless stimulus after each taste in Experiment 2 to serve as a rinse. Here, we found performance to be highest for the last item in a set (recency effect), which is incompatible with habituation. However, we cannot exclude that effects of a release of adaptation compensated detrimental effects of attentional interference.

Finally, another source of encoding-related distortions was the potential role of crossmodal cues, including verbalized encoding of the taste qualities. Participants were instructed not to name the stimuli and confirmed this during debriefing. Nevertheless, participants might have named each presented taste and then judged whether the probe corresponded to one of the previously presented items. However, in both Experiments 1 and 2, recognition accuracy was systematically modulated by the stimuli's chemical similarity, which was inconsistent with a purely verbal encoding of the stimuli. Furthermore, in Experiment 1, the reduction in match accuracy of ~13% with increasing disturbances was inconsistent with the ease of remembering a single word over extended periods.

Performance monitoring

Because WM has been traditionally proposed to represent consciously perceived information ([53–55] but see[56]), we tested whether participants were aware of their memory performance through retrospective confidence ratings. We found that confidence tracked recognition accuracy, such that trials with higher confidence also had a higher accuracy in both experiments. While these findings indicate that participants were aware of the gustatory stimuli, it is not evidence that accuracy and confidence were based on the same source of information in memory. The quality of the perceptual experience has been assessed via metacognitive judgments such as confidence ratings, as a measure of performance monitoring and perceptual awareness, and has been shown to track accuracy in numerous, albeit not all, visual WM tasks[57,58]. In Experiment 1, we observed an inversion of the confidence-accuracy link for foil trials, where accuracy was poorer and confidence higher than for match trials. These findings may reflect reduced variability due to greater item-probe similarity, which increases accuracy but decreases confidence[59]. In this context, these findings suggest that confidence ratings indicate subjective uncertainty arising from stimulus-similarity. While the exact mechanisms by which metacognitive judgments about memory are formed remain elusive, a recent visual WM model identified a lawful relation between accuracy and confidence and postulated that confidence reflects the precision of WM representations[60]. Overall, our findings align well with previous observations in visual WM, where metacognitive awareness tracked recognition accuracy, suggesting that participants were monitoring their memory performance, which is crucial for working memory success[57]. It is surprising that participants failed to track that they "dropped" one or more items as the set size increased (Experiment 2). RTs increased with the number of disturbances (on match trials) in Experiment 1 and set size (on foil trials) in Experiment 2. Suppose RTs are treated as an index of decision difficulty where longer RTs indicate high uncertainty.In that case, RT changes with set size in correct foil but not match trials could be interpreted as subjective awareness of similarity-related uncertainty but not awareness of capacity limitations. The observed pattern of the relatively low accuracy, low confidence, and high RTs in match compared to foil trials further corroborates the involvement of stimulus-similarity.

Storage capacity of gustatory WM

In Experiment 2, we observed a monotonic decrease in recognition accuracy with increasing set size. This result is in line with findings from other modalities (e.g. vision[6,23] or verbal[2,61,62] WM) and can be interpreted as an indicator for a limited gustatory WM capacity. However, a set-size-dependent reduction of accuracy is insufficient to unequivocally deduce whether working memory is constrained by limited shared-resources[20,21] or a slot-based fixed item limit[22,23]. To address this question, we examined recognition accuracy at different positions (relative to the probe) within the sets. While most items were recognized with above-chance accuracy, this was not the case for item 3 in set size 4 and items 2 and 3 in set size 5, indicating that these items were lost from memory, possibly due to capacity constraints. The observed serial-position effects clearly show that some items are represented at a better resolution than others, which is incompatible with an ensemble effect; the latter would predict equal performance, or deterioration thereof, for all items in a set[20,21,25]. Instead, a slot-based limited item model, according to which the maximum number of stimuli is discretely and with adequate resolution represented[22,23,63,64], better explains the observed working memory performance. It is also possible that our results reflect the loss of unattended information in gustatory WM. If each new item reduces and eventually exceeds the available attentional resources, then the unattended items may be degraded to an extent where recognition is rendered impossible.

Furthermore, we found that trial type (match or foil) was a significant modulator of how recognition accuracy changed with set size, such that the set-size dependent accuracy decrease was mostly driven by foil and not match trials. This variation in recognition accuracy between trial types is not readily explained by a slot-based limited item model which would predict a comparable performance on foil and match trials. However, based on the observed stimulus-similarity effects, it is plausible that stimulus-similarity could have contributed to, if not caused, the set-size dependent accuracy decrease because its effect would be more likely to occur in larger sets and affect foil trials more than match trials. Stimulus-similarity would, however, reflect the resolution of representations rather than the number of items that can be remembered[63,65]. Taken together, our results advocate a hybrid model of gustatory WM with a limited number of slots where items are stored with varying amounts of precision (see Schurgin & Brady[66] for a similar argument).

Methods

Participants

Twenty one healthy adults aged between 22 and 42 (15 females; mean = 28.43; SD = 3.90) participated in Experiment 1 and twenty healthy adults aged between 22 and 33 (9 females; mean = 26.60; SD = 3.31) participated in Experiment 2. In Experiment 2, one participant failed to detect all bitter taste trials in the taste detection task and hence was excluded from continuing in the study. Participants reported being generally healthy. They had a Body Mass Index < 28, no current or past neurological disorders or taste disturbances, and did not take medication known to influence brain function or perception. Female participants reported not to be pregnant. All participants signed an informed consent form before participation and received monetary compensation upon completion. The study was approved by the ethical review board of the [name and reference number to be added after review] and complied with the revised declaration of Helsinki.

Stimuli and Apparatus

Stimuli were based on four aqueous solutions prototypical for the basic tastes, sweet, salty, sour, and bitter. They were produced by filling up 190g sucrose (from a local supermarket), 30 g sodium chloride (from a local supermarket), 9 g citric acid (Sigma Aldrich, CAS: 77-92-9), and 0.25g quinine hemisulfate salt monohydrate (Sigma Aldrich, CAS: 207671-44-1) with distilled water to 1L, respectively. The four taste solutions were then mixed at a 1:1 ratio to achieve six binary mixtures: sweet-salty, sweet-sour, sweet-bitter, salty-sour, salty-bitter, sour-bitter. Artificial saliva was prepared by filling up 0.92g sodium bicarbonate (Euro OTC Pharma GmbH, Article Number: 178900) and 0.105g potassium chloride (Euro OTC Pharma GmbH, Article Number: 162070) to 1L with distilled water. Artificial saliva served as a rinse after the tastants and at the same time as non-gustatory, oro-somatosensory distraction because it is typically described to be tasteless [67]. All solutions were stored in the refrigerator at 4°C when not in use and renewed every 72 hours.

Stimuli were delivered by a high-precision computer-controlled syringe pump system[68]. We used five syringes – one for each of the four basic tastants and one for artificial saliva. Each syringe was connected to an inlet tubing that supplied the syringe with the tastant from a glass reservoir and an outlet tubing (288 cm long; 1.59 mm inner diameter, 3.18 mm outer diameter) that delivered the tastants to the participants. Each outlet was mounted in a manifold with 5 inlets (one for each solution) and 1 outlet that had an outlet 1-2 mm stub, which was placed on participants' tongues.

Stimuli were delivered by two syringes at any given time at an individual flow rate of 1.75ml/s during 2s. This resulted in a total flow rate of 3.5ml/s and 7ml volume for each stimulus. This approach enabled us to mix any two tastants "online" during the experiment. To keep the procedure consistent for all stimuli, we also used two syringes to deliver "pure" tastants, which were produced by the simultaneous supply by a "taste" and a "saliva" syringe.

The experiment was controlled by PsychoPy version 3.0.6[69] running on Windows 10. Responses were recorded using a three-button response box (The Black Box Toolkit, Sheffield, UK) that was comfortably placed in front of participants between the outlet nozzle and the screen.

Experimental procedure

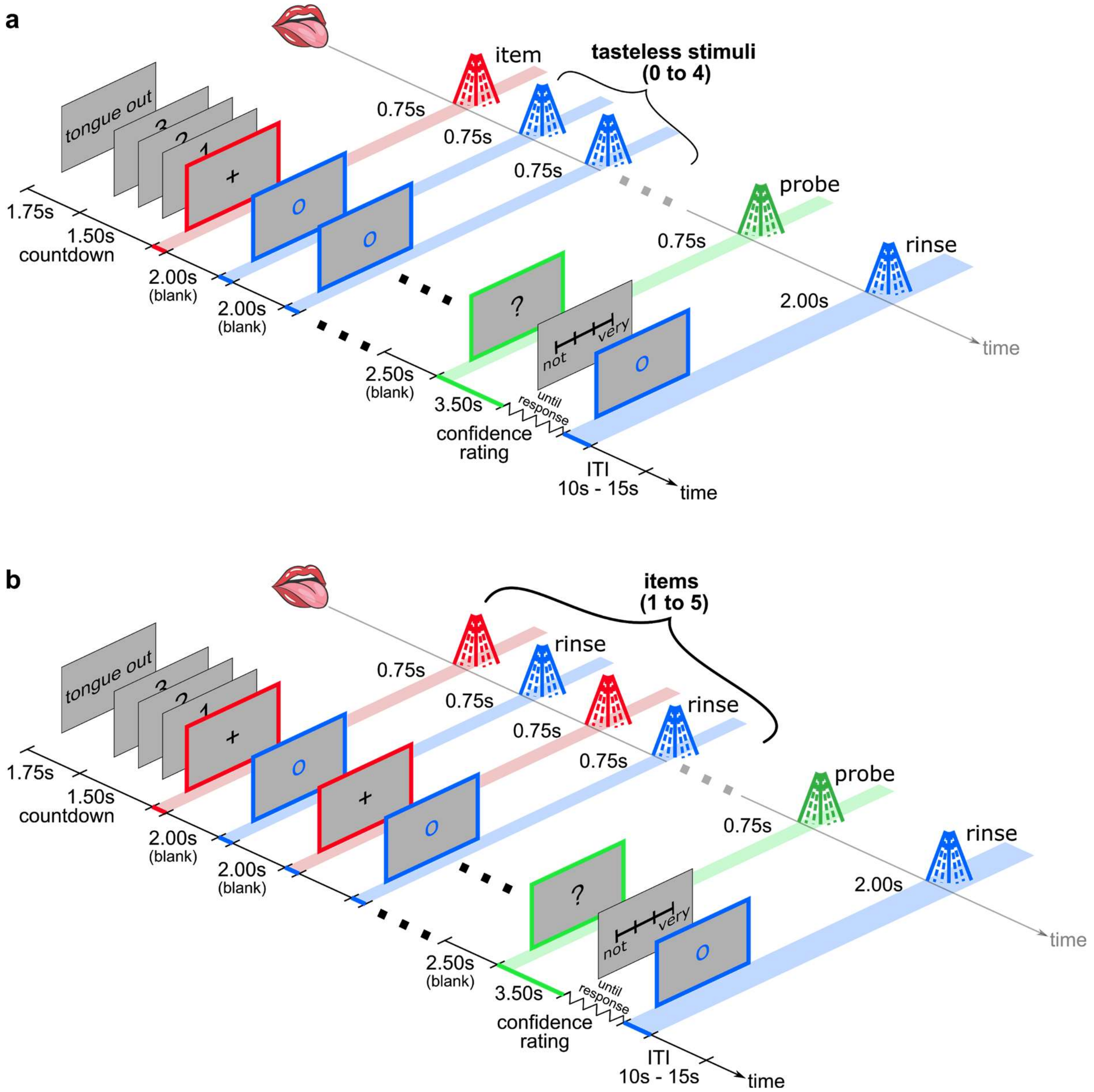

Fig. 5 | Procedure of a single trial. **a,** In Experiment 1, participants received an item and a probe tastant that could be identical (match) or different (foil). Item and probe were interleaved with zero to five tasteless stimuli that served as a cross-modal disturbance. Participants were to indicate by button press whether the item and probe matched. **b,** In Experiment 2, one to five items were sequentially presented. A rinse separated the items. Participants were to indicate whether the probe matches with any of the items in the set. In both experiments, participants rated the confidence of their decision on a 4-point numeric scale (1=not confident, 4=very confident). Colored lines on the timeline represent the duration of the visual display. Shades represent the duration of the spray. Taste stimuli are shown in red, the tasteless rinse in blue, and the probe in green. Colors are not displayed in the experiment and only shown for clarity.

Both experiments consisted of two tasks: a taste detection and evaluation (TDE) task and a taste recognition task with a single item in Experiment 1 and with multiple items in Experiment 2. Experiment 1 lasted 6 hours and was split into two sessions on separate days no more than 14 days apart. In each session, participants performed the TDE task before the single-item taste recognition task (SIR). Experiment 2 lasted 7 hours and was split into three sessions. During session 1, participants completed the TDE task and performed the multi-item taste recognition task (MIR) during sessions 2 and 3.

The TDE task served to ensure that the participants were able to taste all stimuli. For this, we presented the 10 tastants (repeated four times each) and artificial saliva (repeated 12 times) resulting in a total of 52 trials. Each trial began with the visual cue "Tongue out". This cue was presented for 0.75s on the screen, followed by a 3-2-1-countdown (from 3 - 2 -to 1) over 1.5s. Next, a central fixation cross appeared on the screen concurrently with stimulus delivery for 0.75s. After the stimulus presentation, participants were prompted to indicate whether they tasted anything by pressing the response box's left or right button to answer yes or no. Participants were then cued to rate the intensity and pleasantness of the stimulus by moving an arrow with the buttons along on horizontal 11-point scales anchored with "Not at all" and "Very intense" for intensity and with "Unpleasant" and "Very pleasant" for pleasantness. The trial ended with a presentation of artificial saliva (henceforth referred to as rinse) for 2s to remove any residual tastant before the next trial, which started after a varying inter-trial interval (ITI) of 10s to 15s.

In the SIR, a tastant (item) was followed by one to five tasteless artificial saliva stimuli, which served as cross-modal, oro-sensory disturbance, over brief intervals before a second tastant (probe) was presented (Fig. 5 or 6a). On one-sixth of the trials, the probe could occur directly after the item. Participants were to indicate whether the probe was identical to (match) or different (foil) from the item and rate how confident they were when making their decision. Overall, the task comprised 400 trials with match and foil evenly distributed over five different numbers of disturbances. Like the TDE task, each trial began with a cue "Tongue out" and a countdown. Next, simultaneously with a central black fixation cross presentation, participants received a tastant for 0.75s followed by a blank screen of fixed inter-stimulus-interval (ISI) of 2s. On trials with a disturbance, one or more tasteless stimuli were presented next, together with a central blue fixation circle, for 0.75s followed by a 2s ITI. After the last stimulus on a trial and an additional 0.5s delay, the probe was presented for 0.75s together with a question mark on the screen. Participants had 3.5s to respond by button press whether item and probe were the "same" or "different" from probe delivery on. They were then asked to rate their confidence at the time of response by moving an arrow along a 4-point scale anchored with "Not at all" (left) to "Very" (right). The trials ended with a rinse presented for 2s, and the next trial started after a varying ITI of 10 to 15s.

In the MIR, one to five tastants (items) were sequentially presented over brief intervals (up to 28 seconds) before the probe tastant was given (Fig. 5 or 6b). Items were separated by a tasteless rinse that washed the preceding item off the tongue and served as a cross-modal oro-sensory disturbance. Each of the five set sizes comprised 40 match and 40 foil trials resulting in 400 trials. The procedure was similar to Experiment 1 with the difference that 1) sets were composed of 1 to 5 tastants (items), and 2) items were interleaved with a brief rinse for 0.75s.

During each experiment, participants were seated in an acoustically shielded chamber (Studiobox GmbH, Walzbachtal, Germany) and the gustometer and computers were placed outside to minimize any auditory distractions. Additionally, participants listened to ocean waves (Spotify) through insulated in-ear headphones to minimize auditory cues from the gustometer's valves switching. Participants sat in front of a 22 inch LCD monitor at 55 cm distance with their forehead comfortably resting on a headrest, which also holds the manifold and nozzle in place. During the experiments, participants were to place their tongue's tip on the outlet nozzle upon display of a visual cue. They were to remain in this position until the end of a given trial, indicated on the screen. Participants were allowed to take a sip of water and rinse their mouths during the ITI.

All trial types and conditions were presented in pseudo-random order. In order to minimize potential taste-specific effects WM, i.e., sweet may be more memorable than bitter, we rigorously controlled for taste-specific effects in our randomization of Experiment 2, which applied the following constraints: no repetition of tastants within a set/trial, no repetition of the same set of tastants (irrespective of the order of tastants), no repetition of the target tastant for each serial position and set size (providing an equal distribution of stimuli across positions in all set sizes), uniform distribution of the probes across stimulus space, and subsequent trials shared no more than 2/5 of tastants. Lastly, response buttons were counterbalanced across participants and sessions.

Statistical analysis

Data were analyzed with JASP version 0.12.2[70]. Trials without response were excluded (0.6% in Experiment 1 and 1.2% in Experiment 2). Data were analyzed using rmANOVAs, simple main effects ANOVAs, and paired sample t-test. Greenhouse-Geisser correction was applied in case of violations of sphericity as identified by Mauchly's test. Bonferroni correction was applied to all post hoc pairwise comparisons (two-tailed Student t-test). Corrected p-values and confidence intervals were reported; Cohen's d does not correct for multiple comparisons. The α level was set to 0.05.

In Experiment 1, we used a one-way rmANOVA with the factor *number of disturbances* (1 to 4) for recognition accuracy (Fig. 2a); the factor *similarity* (low, intermediate, high) for proportion of "same" responses (p(same), Fig. 2b); and the factor *confidence* (1 to 4) for recognition accuracy (Fig. 2e). To test whether match and foil trials differed, we used separate two-way rmANOVAs with the factors *number of disturbances* (1 to 4) and *trial type* (match, foil) for recognition accuracy (Fig. 2c), RTs (Fig. 2d), and confidence (Fig. 2f). Significant interactions were followed up with simple main effect analyses if applicable.

In Experiment 2, separate one-way rmANOVA with the factor *set size* (1 to 5; Fig. 3A) and *confidence* (Fig. 3D) were performed for recognition accuracy. To test whether match and foil trials differed, two-way rmANOVAs with the factors *set size* (1 to 5) and *trial type* (match, foil) were performed for recognition accuracy (Fig. 3b), RTs (Fig. 3c) and confidence (Fig. 3e). To test for the serial-position effects on recognition accuracy, we performed separate one-way rmANOVAs for set size 5 (5 levels), 4 (4 levels), and 3 (3 levels). Lastly, we performed a paired t-test by testing an alternative hypothesis of μ>0.5, to see if each position in a set size is significantly higher than chance level.

Data availability

The datasets generated during the current study will be made available upon publication in the Zenodo repository.

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Figures

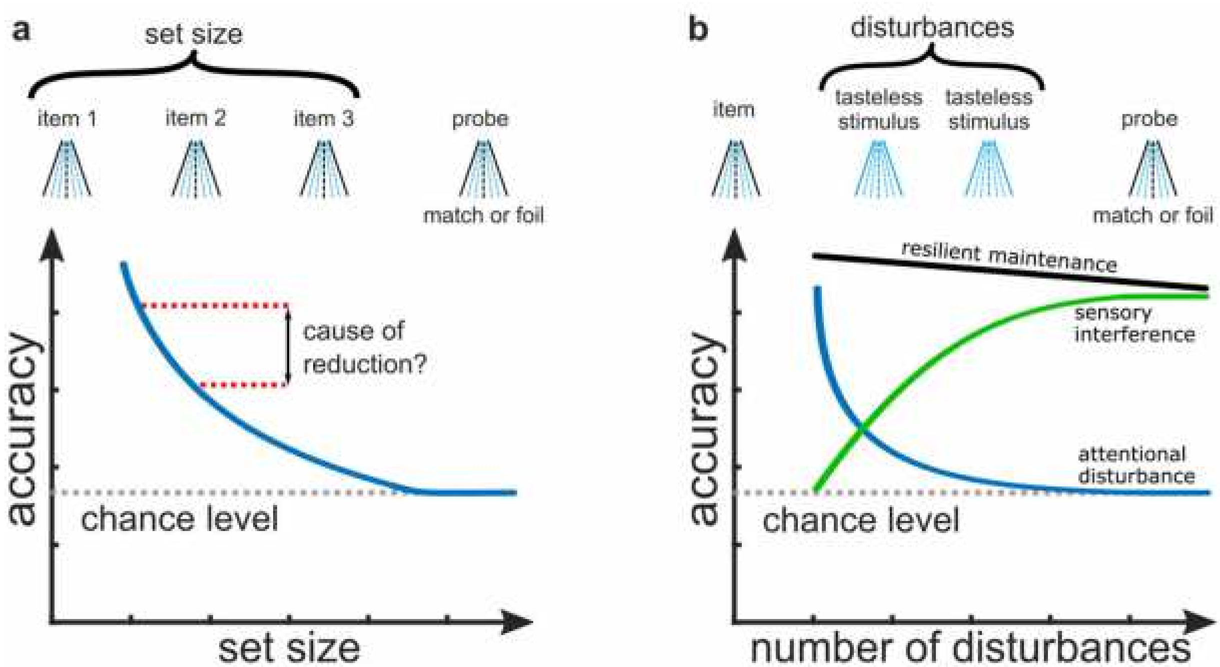

Figure 1

Illustration of hypothetical outcomes and inference effects in estimating taste WM capacity.

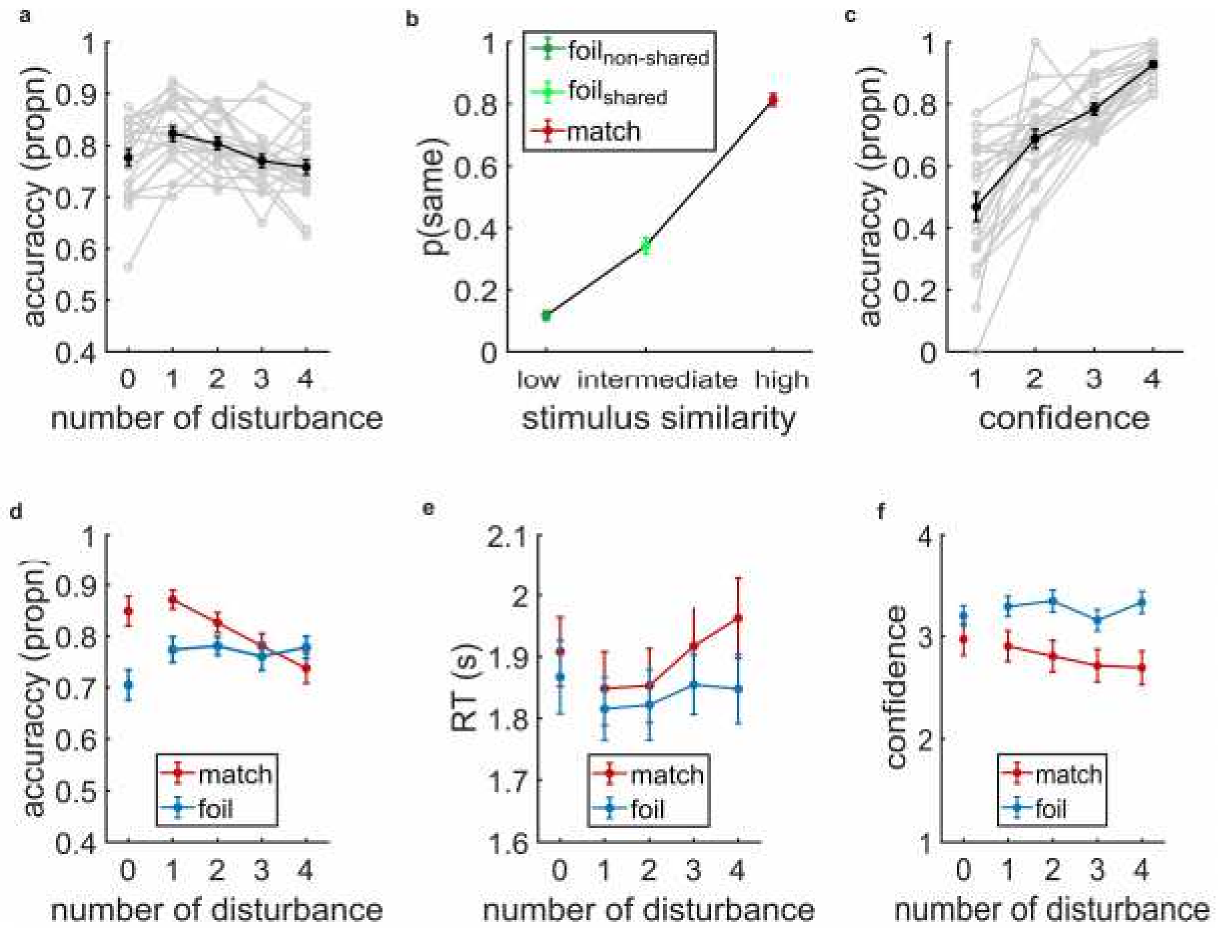

Figure 2

Experiment 1.

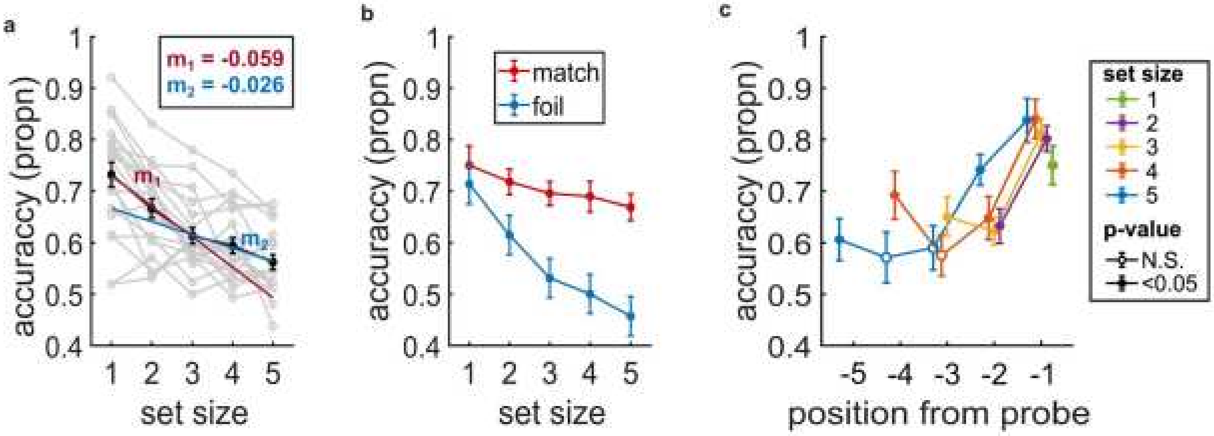

Figure 3

Recognition accuracy in Experiment 2.

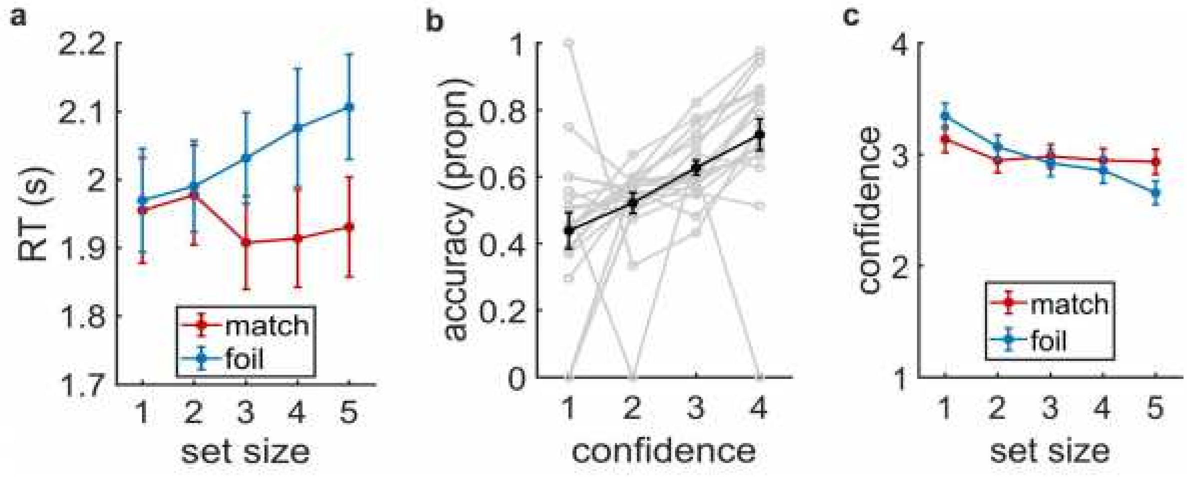

Figure 4

Reaction times and confidences in Experiment 2.

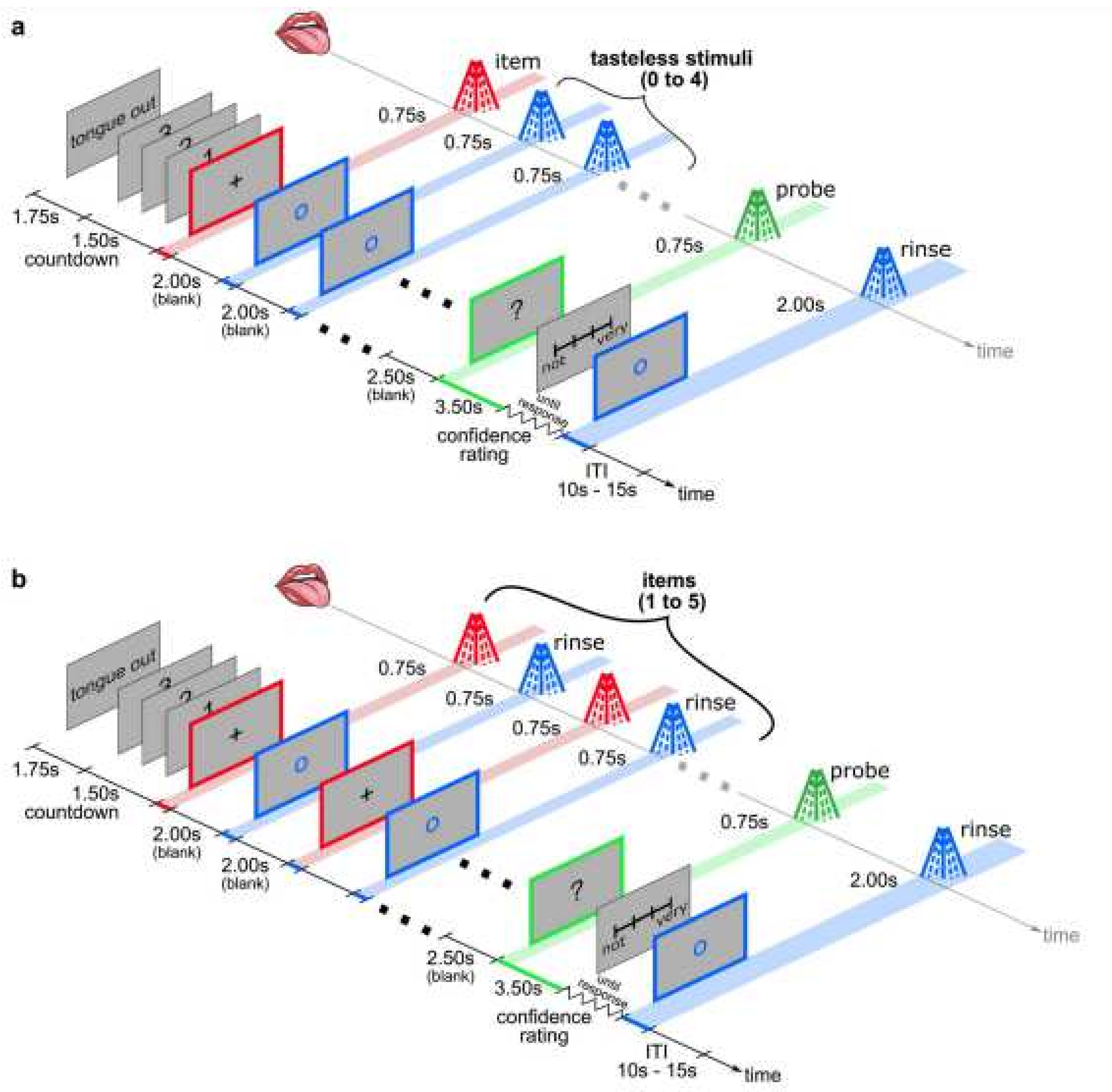

Figure 5

Procedure of a single trial.

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- TasteWMSupplement.pdf