Different olfactory percepts evoked by orthonasal and retronasal odorant delivery

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Abstract

The Duality of Smell hypothesis suggests odorants delivered orthonasally elicit different sensations compared to those delivered retronasally despite activating the same receptors in the olfactory epithelium. Presently, we investigated this further using a matching paradigm free from odorant or semantic memory bias. Subjects were asked to evaluate an aroma delivered in one condition (orthonasal or retronasal delivery) and match the same aroma from four unknowns evaluated in the same or different delivery condition. Panelists matched flavors in four delivery conditions: orthonasal-orthonasal, retronasal-retronasal, retronasal-orthonasal, and orthonasal-retronasal. For orthonasal presentation, panelists smelled samples using their nostrils, and for retronasal presentation, panelists swallowed aqueous flavors. In experiment 1, panelists were instructed to match familiar flavors (banana, grape, orange, raspberry). In experiments 2 and 3, panelists used the same experimental design with either four unfamiliar flavors (kinnow, longan, pawpaw, prunus) or four distinct subtypes of a strawberry flavor (woody, green, ripe, candy). In experiment 1, the number of correct matches in each condition did not significantly differ suggesting stability in the perceptual construct across delivery routes. However, in experiments 2 and 3, significantly more samples were correctly matched in the orthonasal-orthonasal and retronasal-retronasal conditions compared to the retronasal-orthonasal or orthonasal-retronasal conditions suggesting aroma perception is dependent on delivery route. Additionally, across the four delivery methods, the ability to correctly match flavors decreased as flavor familiarity decreased or similarity increased and may reflect the different cognitive strategies employed by subjects when matching these stimuli. Our results suggest odorant percepts are route-dependent and consistent with the Duality of Smell phenomenon.

Key words: orthonasal, retronasal, olfaction, flavor matching, human

Introduction

Olfactory percepts are generated following the binding of odorant molecules to their cognate receptors in the olfactory epithelium. Odorants gain access to the olfactory epithelium via two routes. Orthonasal stimulation occurs when volatile molecules are delivered to the olfactory mucosa through the nose. When sensed orthonasally, odorants are perceived as originating from the external environment and assist organisms with identification and mate selection while also supplying important information regarding the presence of food and danger (Gibson, 1966). Retronasal stimulation occurs when volatile molecules ingested through the mouth gain access to the olfactory epithelium via the opening created by the velum and dorsal pharyngeal wall. In practice, retronasal aroma transport is complex and is improved by oro-pharyngeal movements such as mastication and swallowing (Burdach and Doty, 1987; Pierce and Halpern, 1996; Buettner et al., 2001) which are, in turn, influenced by bolus size and texture (Buettner et al., 2001). Retronasal transport of volatile chemicals provides rich information regarding ingested foods and beverages and is a primary contributor to food flavor. Interestingly, despite activating the olfactory pathway, perceptions evoked retronasally are often referred to the mouth and described as having taste qualities (Murphy et al., 1977; Rozin, 1982; Green et al., 2012; Lim and Johnson, 2012).

Direct comparisons of orthonasal and retronasal olfactory acuity are difficult to perform. Many studies of retronasal olfaction have employed the use of aqueous solutions of odorant stimuli which additionally activate somatosensory and gustatory pathways (Murphy et al., 1977; Burdach and Doty, 1987; Cerf-Ducastel and Murphy, 2001). More recently, attempts to eliminate somatosensory and gustatory activation has resulted in new methods of retronasal odorant delivery (Pierce and Halpern, 1996; Heilmann and Hummel, 2004; Pierce and Simons, 2018).

Whereas these methods have proven useful by allowing for more direct comparisons of retro- and orthonasal evaluations, stimulation using these techniques is also unnatural and lacks the ecological validity of studies in which retronasal stimuli are delivered as a food or beverage bolus. Moreover, many of the findings observed when employing air-phase retronasal delivery have confirmed earlier studies using aqueous-based stimuli.

Studies comparing orthonasal and retronasal perception have delineated several differences in threshold and suprathreshold properties. Orthonasal thresholds tend to be lower than retronasal thresholds, and perceived intensity is greater when odorants are delivered orthonasally (Voirol and Daget, 1986; Diaz, 2004; Heilmann and Hummel, 2004), although exceptions have been observed (Heilmann and Hummel, 2004; Small et al., 2005). Moreover, adaptation has been observed when odorants are delivered orthonasally but not retronasally (Pierce and Simons, 2018). Similarly, perceptual quality of an odorant appears to differ according to route of delivery. For instance, correct identification of a retronasal stimulus decreases if odorant labels are learned through methods incorporating orthonasal delivery (Rozin, 1982; Pierce and Halpern, 1996). More recently, differential brain responses were obtained using fMRI when the same odorant (chocolate) was delivered ortho- versus retronasally (Small et al., 2005). Taken together, these data support the "Duality of Smell" hypothesis advanced by Rozin (1982) in which an odorant's perception is proposed to depend on the route of delivery (ortho- versus retronasal) and location (external world versus mouth) to which it is referred.

Much of the psychophysical support for the Duality of Smell theory has relied upon identification tasks that are dependent not only upon a subject's inherent sensory acuity, but also on their odorant and semantic memory. Whereas the results of such experiments certainly support the hypothesis that different routes of odorant administration elicit different perceptions, it is unclear to what extent memory issues influenced the results. To obviate the confounding effects of memory associated with identification tasks, we presently used a matching paradigm in which subjects were asked to select one of four unknowns that best matched the perception elicited by a reference stimulus.

In addition to memory, the cognitive strategies employed by a panelist during sensory testing can impact the experimental results obtained (O'Mahony et al., 1994; Tedja et al., 1994). Some strategies have been found to be more efficient and result in improved power to resolve sensory differences (O'Mahony and Rousseau, 2003). Similar effects might be expected in matching tasks. We, therefore, sought to manipulate the strategies employed by panelists during a matching task by varying the familiarity and similarity of flavor stimuli. Given non-similar, familiar flavors, we hypothesized subjects would utilize a relatively efficient "concept" strategy in which a flavor is identified as a match because it is closest to a particular concept or exemplar held in their memory (e.g. banana concept); in this condition, the sensory profiles do not need to match identically. Indeed, when flavors are familiar and easily discriminable (e.g. banana, grape, orange, raspberry), the unknown identified as a match need only be recognizable as fitting the flavor concept to be correctly identified. However, when the flavor stimuli are unfamiliar or similar, a less efficient "profiling" strategy is employed in which selection of a matching flavor requires a subject to identify unique characteristics of each sample and choose that having the most similar sensory profile.

By utilizing a matching paradigm and manipulating the cognitive strategies likely to be used under testing conditions, we sought to determine (1) if olfactory percepts are dependent upon the route of delivery and (2) if the cognitive strategies used to discriminate and/or characterize sensations impacts performance in a flavor matching task.

Methods and Materials

Subjects. Ninety subjects (male=35, female=55) ranging in age from 18-65 years participated in the experiments and were recruited through The Ohio State University Consumer Sensory Testing Center's recruitment database. All protocols were approved by the OSU Institutional Review Board. Subjects reported to be in good health and suffered from no known taste, smell, or memory deficits. Subjects were asked to refrain from eating, drinking, smoking, or chewing gum for 1 hour prior to the experiment. The experimental study lasted approximately 45 minutes and all panelists were compensated $20 at the conclusion of the study. All responses were recorded on a computer interface using Compusense Cloud software (Guelph, Canada).

Materials. Four, fruit-type commercial flavors deemed to be non-similar but familiar to the general American population were selected and included banana, grape, orange, and raspberry (MANE, Cincinnati, OH). These flavors were used in Experiment 1 and expected to elicit use of the "concept" strategy. Four commercially available flavors deemed to be non-similar and unfamiliar to the general American population were similarly selected and included yuzu, papaya, apricot (MANE, Cincinnati, OH), and longan (Givaudan, Cincinnati, OH). Yuzu, papaya, and apricot flavors were labeled respectively kinnow, pawpaw, and prunus to ensure complete unfamiliarity with the associated perceptions. These flavors were used in Experiment 2 and were expected to elicit the use of the "profiling" strategy. Finally, four strawberry flavors having similar but distinct sensory profiles were selected for use in Experiment 3 and were expected to elicit the use of the "profiling" strategy. Flavor profiling differentiated each of these flavors as being predominantly woody (Natural Flavor Strawberry, MANE, Cincinnati, OH), green (Natural Strawberry Flavor FAPM042, Wild Flavors, Erlanger, KY), ripe (Natural Strawberry Flavor FAPM041, Wild Flavors, Erlanger, KY), or candy (Artificial Candy Strawberry, MANE, Cincinnati, OH). The four associated flavors were presented as Strawberry A, Strawberry B, Strawberry C, and Strawberry D, respectively to promote use of the "profiling" strategy.

Flavors used for orthonasal evaluation were cut in distilled water, placed into individual capped glass vials, and wrapped in foil to eliminate color bias. Concentrations used evoked perceptions that were approximately isointense across all flavor types (Table 1). Flavors used for retronasal evaluation were dissolved in distilled water at concentrations used commercially in flavored waters, and served in black 2 oz. cups (Dixie, P020BLK) to eliminate any apparent color differences. All orthonasal flavor stimuli were used at final concentrations that evoked intensities approximately equal to those perceived in retronasal evaluations. Isointensity levels were determined by a small preliminary panel (n=10) and all stimuli were described as moderately intense on a five-point category scale (0=barely perceptible; 1=weak, 2=moderate; 3=strong, 4=very strong).

Experimental protocol.

Experiment 1—Familiar flavors. 30 subjects (male=11, female=19) participated in four randomized and counterbalanced sessions. Session ON-ON consisted of orthonasal-orthonasal comparisons, session RN-RN consisted of retronasal-retronasal comparisons, session ON-RN consisted of orthonasal-retronasal comparisons, and session RN-ON consisted of retronasal-orthonasal comparisons. In session ON-ON, subjects were seated comfortably in a traditional sensory booth. They were presented with a tray of samples, each vial containing 10 mL of stimulus. The reference vial was labeled with the name of the flavor and the unknown vials were labeled with 3-digit random numbers. Subjects were instructed to smell the first reference (randomly selected from banana, grape, orange, and raspberry) and choose the sample from the four presented unknowns that best matched the reference (e.g. "Smell the banana flavor, now identify the banana flavor from amongst the four unknowns"). Subjects could evaluate any of the samples as many times as needed and recorded their selection via computer interface. After recording their selection, subjects would repeat the task with the second reference. This process continued until all four references were evaluated. All samples were randomized and counterbalanced.

In session RN-RN, the same guidelines were followed; however, subjects made their evaluations based on retronasal perceptions after swallowing. Each cup contained 30 mL of flavored water, however, subjects were not required to consume the entire contents and were able to request more sample as needed. Similar to session ON-ON, subjects evaluated the reference cup and each of the unknowns and selected the matching stimulus by clicking on the appropriate 3-digit code via the computer interface. Subjects were asked to rinse with water between samples. This process continued until all four references were evaluated. All samples were randomized and counterbalanced.

In session ON-RN, the reference sample was always the orthonasal stimulus and the unknown samples were always presented retronasally. Reference samples (10 mL) were presented in glass vials clearly labeled with the appropriate flavor. Subjects were asked to orthonasally evaluate the reference sample, then swallow the unknown solutions and select the unknown sample that evoked a perception matching that evoked by the reference sample (e.g. "Smell the banana flavor, now taste the unknowns and identify the one that matches the banana flavor). Subjects continued through this process until all four references were evaluated. All samples were randomized and counterbalanced.

In session RN-ON, the reference sample was always presented retronasally and the unknowns were presented orthonasally. Reference samples and unknown samples followed the protocol for retronasal and orthonasal delivery respectively. Subjects were instructed to taste the reference sample, smell the unknowns, and identify the unknown that matched the reference. All samples were randomized and counterbalanced.

Experiment 2—Unfamiliar flavors. 30 subjects (male=12, female=18) participated in four sessions that were randomized and counterbalanced and consisted of the following evaluations: ON-ON, RN-RN, ON-RN and RN-ON. As done in Experiment 1, reference stimuli were labeled with the flavor name (kinnow, longan, pawpaw, and prunus) and the unknown samples were labeled with 3-digit numbers. For all four sessions, data were collected and subjects performed the same tasks as described in experiment 1 (see above).

Experiment 3—Strawberry flavors. 30 subjects (male=12, female=18) participated in four sessions that consisted of the same ON-ON, RN-RN, ON-RN and RN-ON flavor evaluations. Reference stimuli were labeled with the flavor name and a corresponding letter (Strawberry A, Strawberry B, Strawberry C, and Strawberry D). The unknown samples were labeled with 3-digit numbers. For all four sessions, data were collected and subjects performed the same tasks as described in experiment 1 (see above).

Data analysis. Binomial analysis was used to determine whether a significant proportion of subjects correctly identified the matching flavors in each of the four matching conditions. McNemar's test was used to determine whether the distribution of responses differed significantly across route of administration and whether any particular flavor was more difficult to match in each of the three experimental conditions. Chi-square was used to determine whether the distribution of responses differed significantly across cognitive strategy employed. All data are presented as counts or percentages. An $\alpha < 0.05$ was taken as significant.

Results

Experiment 1—Familiar flavors. Familiar, non-similar flavors were used to elicit the "concept" strategy. Overall performance of correct flavor matches was above 70% for all four sessions (range 71-80%; Figure 1A). The differences observed for total number of correct flavor matches in each session was not significantly different (ON-ON:RN-RN, p=0.627; ON-ON:ON-RN, p=0.720; ON-ON:RN-ON, p=0.080; RN-RN:ON-RN, p=1; RN-RN:RN-ON, p=0.296; ON-RN:RN-ON, p=0.121), indicating that when using the efficient "concept" strategy, panelists are able to identify flavor stimuli as matches irrespective of whether those stimuli are delivered orthonasally or retronasally. As shown in Figure 2A, the plurality of panelists got all four flavor matches correct in each session.

Although there was no difference in the number of familiar flavors correctly matched when comparing the congruent and incongruent conditions, the proportion of subjects performing better in the congruent session compared to the incongruent session approached significance (p=0.061; Table 2). We speculate that the deficiencies observed in performance in the incongruent conditions (ON-RN and RN-ON), while not significant, are attributable to perceptual differences elicited via different routes of stimulus administration. However, these perceptual differences are compensated for by the use of the more efficient "concept" strategy that is cognitively less demanding.

Experiment 2—Unfamiliar flavors. Unfamiliar, non-similar flavors were used to promote the use of the "profiling" strategy. Overall performance was not significantly different (p=0.771) between the two congruent sessions with 72% and 69% of flavors correctly matched in the ON-

ON and RN-RN conditions, respectively (Figure 1B). A decrease in performance was observed in the incongruent sessions as there were fewer correct matches (ON-RN: 58% and RN-ON: 59%). Whereas the number of correct matches in the two incongruent conditions did not significantly differ from each other (p=0.878), performance did significantly differ from that observed in the congruent conditions (Figure 1B). Indeed, the overall performance of the ON-ON condition was significantly better from the overall performance in the ON-RN (p=0.030) and RN-ON (p=0.049) conditions. The performance in the RN-RN condition was significantly better than the ON-RN (p=0.049) but not the RN-ON condition (p=0.104). The significant difference between the congruent and incongruent sessions indicates that the same aroma stimuli delivered orthonasally and retronasally elicit differing sensations that is unmasked by the use of unfamiliar flavors which requires utilization of the more cognitively demanding “profiling” strategy.

A significant majority of subjects individually performed better in the congruent sessions than the incongruent sessions (Table 2; p=0.031, 1-tail) confirming the matching task was significantly more difficult when the aroma stimuli were delivered via different routes. Similarly, in comparison to the performance observed when utilizing the “concept” strategy, there were fewer correct matches across all delivery conditions when subjects relied on the “profiling” strategy; such an effect resulted in a leftward shift of the matching frequency distribution curve (Figure 2B).

Experiment 3—Strawberry flavors. Familiar, similar flavors were used in experiment 3 to encourage the use of the “profiling” strategy and to additionally investigate the impact of similarity among stimuli on performance. Overall performance of correctly identifying flavor matches decreased in comparison to the familiar and unfamiliar experiments (Figure 1C). As observed using unfamiliar flavors, the congruent flavor matching sessions resulted in similar performance (ON-ON: 65% and RN-RN: 60%; p=0.450). Additionally, no significant difference in the number of correct matches was observed between the incongruent sessions (ON-RN:53% and RN-ON: 46%; (p=0.260). However, when comparing performance between the congruent and incongruent conditions, significant differences were observed. The number of correct matches in the ON-ON condition was significantly higher than in the ON-RN condition (p=0.05) and RN-ON condition (p=0.004). In contrast to the results from the unfamiliar experiment, the RN-RN condition was significantly different than the RN-ON condition (p=0.039) but not the ON-RN condition (p=0.320), which may reflect subject diversity between the two experiments. Overall the decrease in performance from the congruent to the incongruent sessions indicates (1) percepts evoked orthonasally and retronasally by the same stimuli are different and (2) the increased cognitive load associated with profiling similar flavors significantly impacts matching performance.

Consistent with the results from experiment 2, a significant majority of subjects individually performed better in the congruent sessions than the incongruent sessions (Table 2; p<0.002, 1-tail) confirming the matching task was significantly more difficult when stimuli were delivered via different routes. Similarly, subjects generally made fewer correct flavor matches within each testing condition resulting in a further leftward shift of the matching frequency distribution curve (Figure 2C).

Cognitive strategies. Stimulus characteristics (flavor familiarity and/or similarity) disposed subjects to utilize specific cognitive strategies (concept strategy or profiling strategy) when identifying flavor matches, however, the use of any given strategy was presumed to be independent of the route of stimulus delivery. We hypothesized that the concept strategy (Figure 1A) was more efficient relative to the profiling strategy (Figure 1B and C) due to decreased cognitive load. Statistical analyses supported this assertion. When comparing across all flavor types (familiar, unfamiliar, strawberry), a significantly higher number of subjects correctly identified flavor matches in the familiar flavor condition (concept strategy condition) as compared to the unfamiliar and strawberry flavor conditions (χ=10.41 and 28.45 respectively, df=3, $p<0.02$). This proved to be the case for all routes of delivery. The distribution of responses obtained between the unfamiliar and strawberry flavor conditions were not significantly ($p>0.05$) different (χ=5.68, df=3).

Flavor difficulty. In each of the three experimental conditions, we assessed whether any particular flavor was most difficult to match. In Experiments 1 and 3, we found no evidence of this (Figures 3A and C). For Experiment 1, no flavor (banana, grape, orange, and raspberry) was incorrectly matched significantly more often although the difference between raspberry and orange approached significance (Table 3). Similar results were obtained with the four strawberry flavors (woody, green, ripe, and candy; Table 3). However, in the unfamiliar flavor condition, prunus (apricot) was found to have significantly (see Table 3B for p-values) fewer correct matches (Figure 3B) compared to all of the other stimuli [kinnow (yuzu), longan, and pawpaw (papaya)]. We are uncertain why prunus was most difficult to match and speculate that it may reflect the complexity of this stimulus.

Discussion

The qualitative content of olfactory percepts are route dependent. Across all three flavor types (familiar, unfamiliar, and strawberry) subjects correctly matched more flavors when delivered by the same route (ON-ON or RN-RN) than when delivered by different routes (ON-RN or RN-ON). Additionally, subject performance decreased as flavor familiarity decreased or as flavor similarity increased. These results suggest that in addition to route of delivery, semantic labels and cognitive strategies employed during matching tasks influenced subject performance when trying to identify flavors.

Orthonasal-retronasal perception. We found subjects were better able to identify matching flavors when both the reference and the unknowns were presented via the same route. Prior studies have indicated differences in the processing of olfactory information depending on whether odorants are delivered ortho- or retronasally. Whereas we recently reported that adaptation to an olfactory stimulus is route-dependent (Pierce and Simons, 2018), others have shown that both intensity (Heilmann and Hummel, 2004; Visschers et al., 2006) and quality (Rozin, 1982; Bojanowski and Hummel, 2012) of olfactory perceptions also depend on route of administration. Consistent with these findings, comparison of brain activity exhibited during orthonasal and retronasal aroma delivery resulted in different neural response patterns (Small et al., 2005). Interestingly, patients with documented orthonasal olfactory loss but intact taste were found to have normal retronasal olfaction as confirmed psychophysically and electro-physiologically (Landis et al., 2005). Collectively, these results support the Duality of Smell hypothesis (Rozin, 1982).

Differences between orthonasal and retronasal perception have been attributed to variations of air-flow patterns (Zhao et al., 2006) as well as non-uniform receptor distributions across the olfactory mucosa (Schoenfeld and Cleland, 2006). Alternatively, selective adsorption of odorant molecules to the oral (Linforth et al., 2002) or lung (Verhagen, 2015) mucosa during retronasal evaluations may alter retronasal odor concentrations and/or the odor mixture make up prior to ascent into the nasal sinus. Similarly, different odorant concentrations or altered chemical composition in the headspace could result from thermal changes associated with placing the stimulus in the mouth (Roberts and Acree, 1995) or differential enzymatic activity in the oral cavity compared to the nasal sinus (Pagès-Hélary et al., 2014). Rozin (1982) has suggested the presence of a palpable oral bolus may also enable a differentiating gating mechanism. However, differential quality percepts were observed between the different pathways even when retronasal stimuli were delivered via nasal cannulae that limited interaction of the odorant with the oral cavity (Heilmann and Hummel, 2004).

Cognitive strategies. In many prior studies comparing orthonasal and retronasal olfaction, particularly identification tasks, the results were confounded by protocols that required subjects to engage memory processes. Therefore, it was unclear the extent to which differences in orthonasal and retronasal perception were due to route of stimulus delivery or, alternatively, deficits in semantic or olfactory memory.

To overcome some of these limitations, we adopted a "memory-free" methodology in which subjects were asked to evaluate a reference stimulus and then identify the matching stimulus from a set of unknowns. Utilization of this method eliminated the reliance on semantic memory because subjects were not required to memorize or recall labels as done in prior studies (Rozin, 1982; Sun and Halpern, 2005). Additionally, subjects could assess the sample as many times as needed and therefore were not required to memorize the perceptual qualities of the evaluated stimuli. Using such a paradigm, the reference and unknown stimuli could be delivered in a congruent fashion (ON-ON or RN-RN) or an incongruent fashion (ON-RN or RN-ON) enabling the ability to assess the impact of delivery route on flavor matching acuity without the confounds associated with memory and recall. Despite these methodological improvements, subjects still found it difficult to identify matching stimuli when the flavors were delivered by different routes (ON-RN and RN-ON). Even as panelists showed perfect acuity when reference and unknown flavor delivery was consistent (ON-ON and RN-RN), they were prone to more errors when those same flavors were delivered via differing routes (ON-RN and RN-ON).

The results in the familiar flavor treatment did not support the Duality of Smell hypothesis. Our results suggest that when evaluating familiar flavors, subjects are able to compensate for the differences in perceptual quality resulting from orthonasal versus retronasal administration, and identify flavor matches by comparing to exemplars held in their long-term memory. Thus, as reported in other psychophysical tasks (O'Mahony et al., 1994; Tedja et al., 1994; O'Mahony and Rousseau, 2003), the cognitive strategies employed by subjects during their evaluations can have a significant impact on panelist performance that could lead to erroneous interpretations of results.

As flavor familiarity decreased or flavor similarity increased, subjects were required to employ alternative cognitive strategies to correctly identify matching stimuli. In such instances, subjects likely sought to identify some characterizing attribute that would allow them to discriminate between flavors. Thus, stimuli having the most similar perceptual qualities would be identified as matching. However, use of this "profiling" strategy proved to be inefficient and resulted in more matching errors. This is true whether the flavors were presented in a congruent (ON:ON or RN:RN) or incongruent (ON:RN or RN:ON) fashion. However, in the incongruent condition, the impact of using the profiling strategy was even more striking as the number of correct matches declined further relative to the congruent condition. Comparable results were obtained in the third experimental condition where subjects were required to match 4 similar, but distinct, strawberry profiles. In this condition, subjects were required to rely even more heavily upon the profiling strategy to discriminate and match the stimuli. As a consequence, for each delivery condition, performance was even worse when compared to the familiar flavor treatment and likely reflects the increased cognitive load required to profile similar flavors versus matching a flavor to an exemplar. Not surprisingly, when the profiling strategy was used to match flavors delivered incongruently (ON:RN or RN:ON), performance declined further suggesting the same stimuli delivered orthonasally and retronasally evoke different perceptual qualities—an outcome consistent with the Duality of Smell hypothesis (Rozin 1982).

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Table 1. Isointense orthonasal and retronasal concentration levels in water for each cognitive strategy created on a volume-by-volume basis (volume mL flavor/volume mL water).

	Stimuli	**Orthonasal Concentration Level**	**Retronasal Concentration Level**
Familiar	Banana	0.18%	0.28%
	Grape	0.14%	0.23%
	Orange	0.35%	0.40%
	Raspberry	0.05%	0.13%
Unfamiliar	Kinnow	0.25%	0.40%
	Longan	0.25%	0.30%
	Pawpaw	0.20%	0.25%
	Prunus	0.20%	0.25%
Strawberry	Strawberry A	0.33%	0.40%
	Strawberry B	0.20%	0.35%
	Strawberry C	0.25%	0.35%
	Strawberry D	0.30%	0.25%

Table 2. Number of subjects who individually performed better ($p<0.05$) in the respective sessions in the three cognitive strategy experiments.

	Familiar	Unfamiliar	Strawberry
Congruent sessions	18	20	19
Incongruent sessions	9	9	3
Neither	3	1	8
p-value (1-tailed)	0.061	0.031	<0.002

Table 3. Flavor matching difficulty. To determine whether a flavor was most difficult to match in each Experiment, the number of correct matches were compared for each flavor pair using McNemar's test. Values depict the p-values associated with each comparison.

Experiment 1. Familiar Flavors	Banana	Raspberry	Grape	Orange
Banana	---	0.337	0.701	0.597
Raspberry		---	0.597	0.061
Grape			---	0.296
Orange				---

Experiment 2. Unfamiliar Flavors	Kinnow	Longan	Pawpaw	Prunus
Kinnow	---	0.511	0.371	0.001*
Longan		---	0.096	0.020*
Pawpaw			---	<0.001*
Prunus				---

Experiment 3. Strawberry Flavors	Strawberry A	Strawberry B	Strawberry C	Strawberry D
Strawberry A	---	1	0.341	0.780
Strawberry B		---	0.332	0.791
Strawberry C			---	0.603
Strawberry D				---

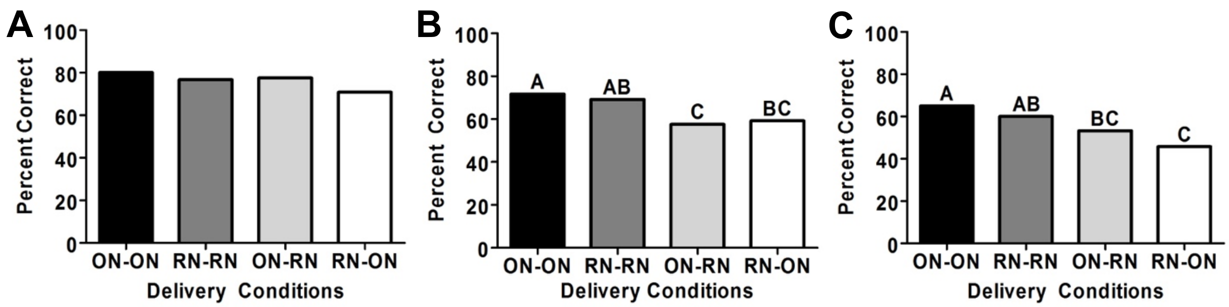

Figure 1. Overall matching performance for each aroma delivery condition in each cognitive strategy experiment. **(A).** Familiar flavors (banana, grape, orange, raspberry) used to elicit use of “concept strategy”. **(B).** Unfamiliar flavors (kinnow, longan, pawpaw, prunus) used to elicit use of “profiling strategy. **(C).** Strawberry flavors (strawberry A, B, C D) used to elicit use of “profiling strategy”. ON-ON: reference and unknown stimuli presented orthonasally; RN-RN: reference and unknown stimuli presented retronasally; ON-RN: reference presented orthonasally and unknowns presented retronasally; RN-ON: reference presented retronasally and unknowns presented orthonasally. Letters above the bars indicate significant differences between each session as determined by McNemar’s test.

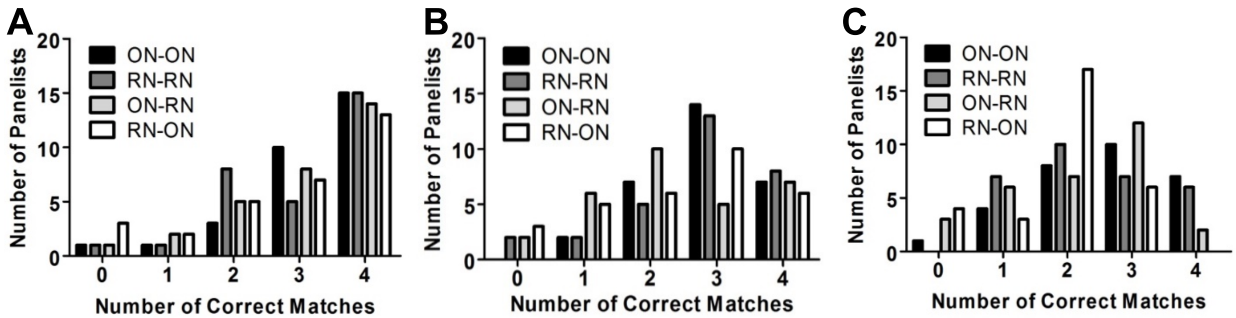

Figure 2. Distribution of correct flavor matches for each aroma delivery condition in each cognitive strategy experiment. **(A).** Familiar flavors (banana, grape, orange, raspberry) used to elicit use of "concept strategy". **(B).** Unfamiliar flavors (kinnow, longan, pawpaw, prunus) used to elicit use of "profiling strategy. **(C).** Strawberry flavors (strawberry A, B, C D) used to elicit use of "profiling strategy". Note, when using the profiling strategy, there are fewer numbers of correct matches as indicated by a general leftward shift of the distribution curve in **(B)** and **(C)**.

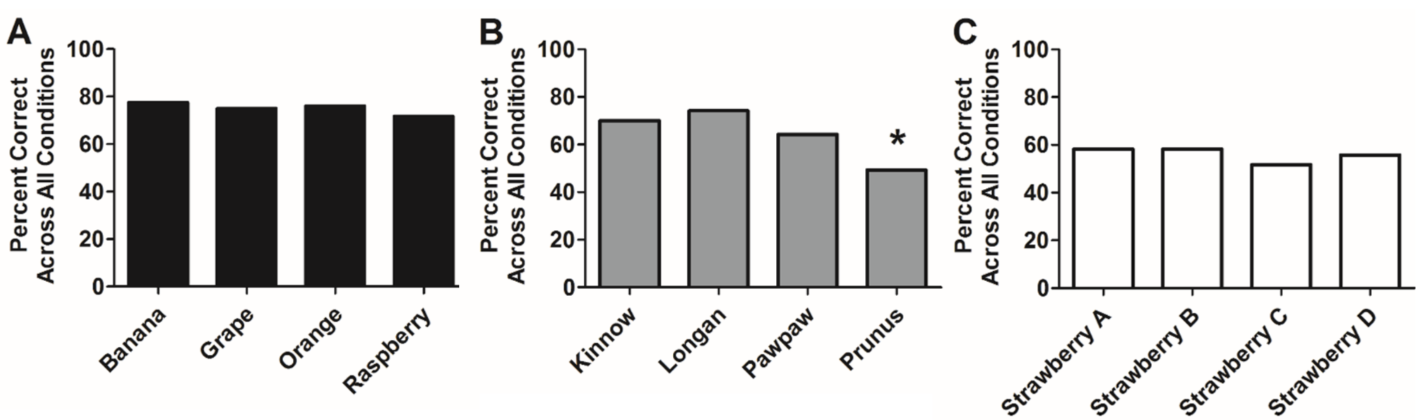

Figure 3. Comparisons of flavor difficulty within each testing condition: **(A)**. Familiar flavors **(B)**. Unfamiliar flavors and **(C)**. Strawberry flavors. In each graph, bars depict the percentage of times that flavor was correctly matched across all delivery conditions. For familiar and strawberry flavors, no particular stimulus was most difficult to match. For unfamiliar flavors, the prunus stimulus was correctly matched significantly fewer times than kinnow, longan and pawpaw stimuli as indicated by the asterisk in **(B)**.