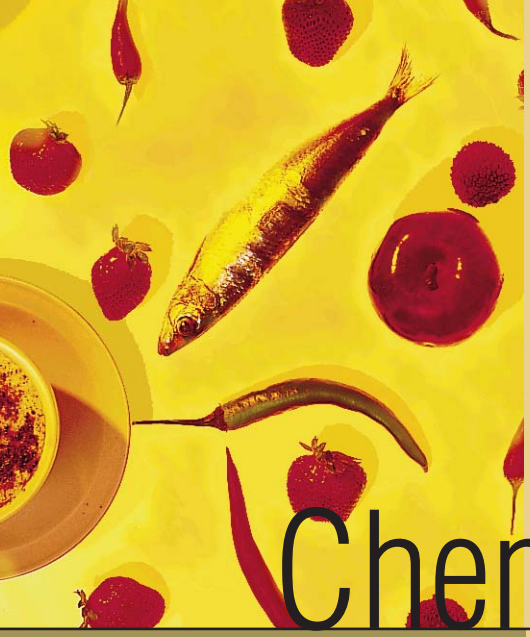

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ChemoSense

Editorial

By Graham Bell
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When you bite into food, or swallow fluid, odorants released from the material travel back into your throat and up into the nasal cavity, reaching your olfactory receptors by the rear passages of your nasal cavity. The process is assisted by pressure from your exhaled breath. This is called retronasal smelling. We return to that subject with another important review by Bruce Halpern. Bruce reviews the models of vapour flow in the nasal cavity and the most recent psychophysical evidence differentiating olfactory perception and its trigeminal contributions coming from orthonasal and retronasal stimulus delivery. This review is important to anyone interested in perception of flavour and appreciation of food.

The number of scientists working on the chemosensory science of

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Mechanisms and Consequences of Retronasal Smelling: Computational Fluid Dynamic Observations and Psychophysical Measures

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Introduction

The flavor of foods and beverages is an amalgam of sensory events originating from the oral cavity, plus vapor phase chemical stimulation entering through the nostrils and pre-consumption visual components (Small and Prescott, 2005). Oral-cavity aspects may include thermal, tactile, and chemical-based stimuli that activate trigeminal and gustatory pathways, and, perhaps, bone-conducted sound. In addition, with each exhalation, vapor phase odorants flow from the oral cavity, typically reaching the nasal cavities and exiting via the

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wine is growing. More wine is being consumed around the world and new producer countries are emerging, such as the UK. Wine from relatively young regions in Australia and New Zealand, such as Orange in NSW, are starting to produce wines of significant quality. Nevertheless, the Barossa and the Hunter Valleys continue to boom. But there are more pressing issues afoot: A recent commentary by Richard Smart, in *The Australian and New Zealand Wine Industry Journal*, deserves your attention, as it reviews papers presented at a recent Global Climate Change conference. It is confirmed that mean temperatures in wine regions have been growing since 1973 and grapes in the Bordeaux region have been getting steadily sweeter. Damaging stress will soon be felt, from heat and scarcity of water, so "Plan for Change" is Richard's take-home message.

The Australasian Association for ChemoSensory Sciences is calling for symposium topics for their Annual Conference in Brisbane in December. Please plan to attend. Send your ideas for symposia, without delay, to Judith Reinhard ■

Mechanisms and Consequences of Retronasal Smelling: Computational Fluid Dynamic Observations and Psychophysical Measures
continued

nostrils. This odorant flow provides the stimulus for retronasal smelling, which arguably is the dominant element for humans of flavor and food-related decisions (Rawson, 2006).

Within the nasal cavities, exhalation-driven retronasal smelling could be expected to utilize the same olfactory and trigeminal receptor arrays as would orthonasal smelling during inhalations (Brand et al. 2001). Consequently, a reasonable hypothesis might be that human orthonasal and retronasal smelling are essentially equivalent (see Pierce and Halpern, 1996). Underlying assumptions could logically include comparable airflow pathways, velocities, and distributions of odorants in the nasal cavities, and psychophysical responses that are similar for orthonasal and retronasal smelling. This review will examine studies in humans that pertain to these assumptions and their overarching hypotheses. These hypotheses posit that knowledge of orthonasal respiratory fluid dynamics is sufficient to understand airflow during human smelling, and that the olfactory system is necessary for smelling.

The concept of orthonasal and retronasal equivalence is rejected for nasal cavity fluid dynamics and nasal cavity odorant conductance, and is at least incomplete for psychophysical responses. With regard to

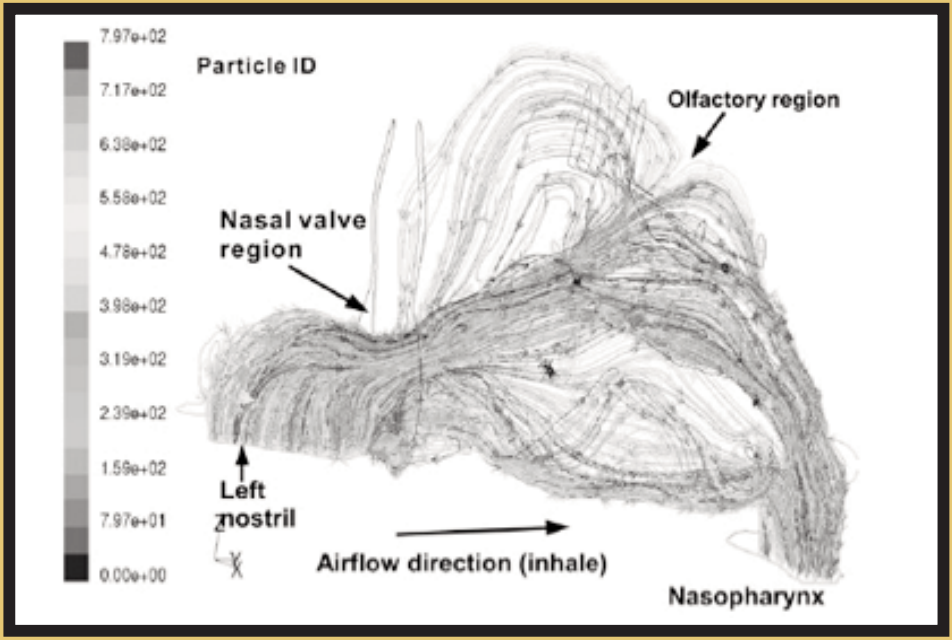

Figure 1. Streamline patterns (the paths traced out by neutrally buoyant particles moving with the fluid flow) for computed (computational fluid dynamics) steady laminar airflow in a human nasal cavity during inhalation, based upon 1 mm nasal computerized tomography (CT) images from one individual's left nasal cavity (10.75 ml volume). Total (global) airflow rate was 103 ml/second. It can be seen from the small number of streamlines that little (2%) of total external naris (Left nostril) airflow passed through the olfactory region. As initially imaged, the olfactory region airflow rate was 1.9 ml/second. For the streamline simulations represented in this figure, the nasal valve region (the "Nasal valve region" label may correspond to the internal nasal valve, see Alvi and Ching, 2004) was narrowed to half of its initially imaged size, which was already narrower than that of the right nasal cavity (see figure 2). This narrowing of the nasal valve region resulted in an enhanced vortex (the circular and elongated flow patterns) in the olfactory region (olfactory cleft). The "Particle ID" scale on the left indicates the number of neutrally buoyant particles whose trajectories were used to plot the streamlines; the small X, Y, Z on the lower left are coordinates from the CT scans, approximately corresponding to sagittal, coronal, and axial directions (personal communication, Kai Zhao, , February 2008). Reproduced from Zhao, K., Scherer, P. W., Hajiloo, S. A., and Dalton, P. (2004). Effect of anatomy on human nasal air flow and odorant transport patterns: implications for olfaction. *Chem Senses* 29: 365-379, Figure 9, with permission of Oxford University Press.

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continued

specifics, airflow patterns and odorant distributions in the human nasal cavities differ between exhalations and inhalations. Psychophysical identifications of odorants upon retronasal stimulation, although often qualitatively similar to orthonasal responses, have oral cavity components not available to orthonasal smelling. Consequently, the oral cavity origin of retronasal smelling may permit a greater potential contribution of the trigeminal system. A broader issue is also raised concerning the role of trigeminal-based responses that utilized the same verbal labels as orthonasal or retronasal smelling.

The review is divided into two main sections, each with several subdivisions: Nasal Cavity Airflow and Distributions of Odorants (Access to olfactory and trigeminal receptors, Global versus olfactory region airflow, Differences between the nasal cavities, Vortices, Odorant Distributions), and Psychophysical Responses (General considerations, Sensory systems, Recent studies).

NASAL CAVITY AIRFLOW AND DISTRIBUTIONS OF ODORANTS

Access to olfactory and trigeminal receptors

Odorant molecules that are dissolved or entrained in respiratory airflow encounter a complex and changeable environment in the nasal cavities (Hornung 2006). Most of this environment is non-olfactory, but may nonetheless present sensory receptors for vapor-phase stimuli. Specifically, for the inspired air that permits orthonasal smelling, approximately 85% to 98% of the airflow does not reach the mucosal regions that provide olfactory receptors (Figure 1, Olfactory region) (Zhao et al., 2004). However, most if not all of the airflow during inhalations can access trigeminal receptors in the nasal cavity (Brand, 2001, 2006). It follows that trigeminal stimuli, if present at sufficient concentrations during inhalations, may be expected to usually produce responses from trigeminal receptors. For exhalations during retronasal smelling, the regions of computed highest local airflow velocity in the nasal cavities differ from those during inhalations (Ishikawa et al., 2006), raising the possibility that nasal cavity responses to trigeminal stimuli have different retronasal and orthonasal signatures.

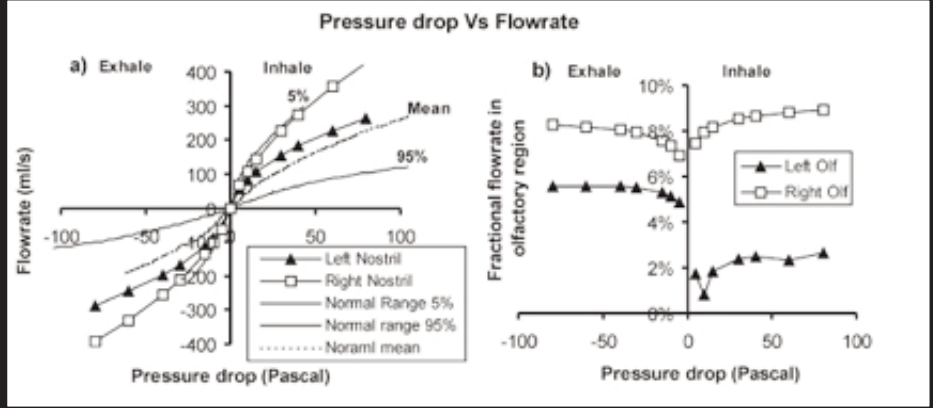

Figure 2. Computed numerical rhinomanometry (measurement of the airflow and pressure within the nose during respiration) of laminar airflow in human nasal cavities, based upon 1 mm nasal computerized tomography (CT) images from one individual (see Figure 1 for a streamline representation). Airflow for steady exhalation and inhalation, for the left (filled triangles) and right (open squares) nasal cavities, was calculated using pre-determined pressure drops. The CT images had indicated that the nasal valve region of the left nasal cavity was partially blocked. This measured difference between the nasal cavities was retained for the computed values of this figure. Relationships between pressure drop and airflow are shown for a) total (global) airflow, and, b) fractional local airflow through the olfactory region, plotted against the pressure drop across the whole nasal cavity (between each external naris and the nasopharynx). It can be seen that total airflow shows little difference between exhalation and inhalation. However, olfactory region airflow exhibited a small effect of airflow direction for the non-blocked, right nasal cavity (Right Olf), and large differences between exhalation and inhalation for the partially blocked (smaller diameter nasal valve region) left nasal cavity (Left Olf). Reproduced from Zhao, K., Scherer, P. W., Hajiloo, S. A., and Dalton, P. (2004). Effect of anatomy on human nasal air flow and odorant transport patterns: implications for olfaction. *Chem. Senses* 29: 365-379, Figure 10, with permission of Oxford University Press.

Global versus olfactory region airflow

The nasal valve. The size of the nasal valve region (i.e., a nasal cavity region or regions of variable high resistance to airflow. See Alvi and Ching, 2004; Halpern 2008, and Figures 1 and 3) will have some effect on global airflow throughout a nasal cavity, but will have proportionally greater consequences for airflow in the olfactory region of a nasal cavity. In general, small changes at the nasal valve region can induce olfactory region airflow modifications one or two orders of magnitude larger than those for overall airflow (Hornung, 2006). For example, a decrease of about 2% in nasal valve region dimensions, although associated with a 19% reduction in computed global air flow throughout the nasal cavity, resulted in a very much larger, 77% decrease in computed olfactory region air flow (Zhao et al., 2004). In this instance, respiratory airflow to nasal cavity mucosa innervated by trigeminal nerve peripheral terminals, although reduced, would change only one-quarter as much as would airflow to the olfactory mucosa of the same nasal cavity. A possible consequence of this could be a relative enhancement of responses to trigeminal odorants.

General considerations. Airflows within a nasal cavity for a wide range of pressure differences between the nostril and the nasopharynx during exhalation and inhalation have been explored using computational analyses (Zhao, et al. 2004) (Figure 2). Because exhalation and inhalation translate into retronasal and orthonasal airflow, these airflow and pressure differences are of direct relevance to potential differences between retronasal and orthonasal smelling.

Global airflow. For an airflow range of 100 ml/second to 200 ml/second, which includes normal resting breathing rates (Kelly et al., 2000), computed global nasal cavity airflows in relation to pressure drops between the nostril and the nasopharynx were very similar for exhalation and inhalation (see Figure 2a). The exhalation airflow rate was computed to be approximately 11.6% greater than the inhalation flow rate (personal communication, Kai Zhao, January 2008). It is unclear if a difference of this size in

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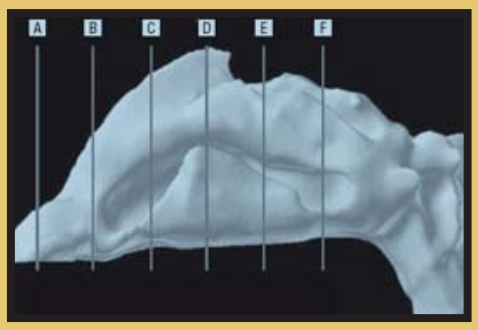

Figure 3. Lateral view of a three-dimensional model of a human nasal cavity and pharynx, constructed using imaging software from 141 1 mm computed topographic (CT) images of one individual. Labeled regions correspond to coronal planes at: A. Nasal vestibule, B. Nasal valve region, C. Anterior portion of the inferior turbinate, D. Anterior portion of the middle turbinate, E. Mid-portion of the middle turbinate, and F. Posterior portion of the inferior turbinate. Reproduced from Ishikawa, S., Nakayama, T., Watanabe, M. and Matsuzawa, T. (2006). Visualization of flow resistance in physiological nasal respiration. Analysis of velocity and vorticities using numerical simulation. *Arch. Otolaryngol Head Neck Surg.* 132: 1203-1209, Figure 4, with permission of the American Medical Association. *Copyright © (2006) American Medical Association*. All Rights reserved.

global airflow rates would be sufficient to produce retronasal versus orthonasal effects.

Olfactory region airflow. Computed fractional local olfactory region flow rates ("local olfactory air flow rate divided by total air flow rate through each nostril", Zhao, et al. 2004) through a human nasal cavity with a normal diameter (neither expanded nor contracted) nasal valve region range between approximately 6.5% and 9% of total airflow (Figure 2b, "Right Olf"). Under these circumstances, during exhalation, computed fractional local flow rates through the olfactory region in relation to pressure drops between the nostril and the nasopharynx are 6.5% to 8.5% of total airflow rate, slightly smaller than the 8% to 9% airflow rates during inhalation. It was suggested that the differences might be " . . . due to the different relative geometrical orientations of the olfactory region to the inlet when flow is reversed." (Zhao et al., 2004), where "the inlet" refers to the nostril and the nasal valve region. That is, in relation to the olfactory region, the nasal valve region would be upstream during inhalation but downstream during exhalation (see Halpern, 2008). These small differences in olfactory region airflow rate could be a factor in the higher thresholds and lower identification accuracies that have been observed for retronasal in comparison with orthonasal smelling during natural breathing (See Psychophysical Responses, below; Halpern, 2004).

In contrast to the small effects of airflow direction, i.e., exhalation versus inhalation, on computed fractional local olfactory region flow rates in the presence of a normal nasal valve region, a modest narrowing of the nasal valve region results in substantial differences between exhalation and inhalation (Figure 2b, "Left Olf") (Hornung, 2006). For example, with an approximately 2% narrowing of the nasal valve region, computed olfactory region airflow rates during exhalation ranged from approximately 4.5% to 5.5% of total airflow rate, but during inhalation, from approximately 1.5% to 2.5% for most pressure drops (Zhao et al., 2004). Thus, with a narrowed nasal valve region, computed fractional local olfactory region airflow rates could more than double during exhalation compared with inhalation.

In addition to nasal valve region effects, vascular changes can alter the dimensions of airflow spaces, and may even cause switches between laminar and turbulent flow (Hornung, 2006). Odorants themselves can rapidly elicit such intranasal vascular changes. These changes may be initiated directly within the nasal cavities by some odorants; via vasomotor pathways after processing in the CNS (e.g., Naida et al., 1996), or by other odorant receptors (e. g., Finger et al., 2003; Gulbransen et al., 2008). Finally, externally applied nasal dilators can substantially modify nasal cavity dimensions, airflow, and orthonasal smelling (Hornung, et al. 2001).

Differences between the nasal cavities

Under in vivo circumstances, the two nasal cavities can present not only dynamic but also non-isomorphic environments for airflow and odorant distribution (Sobel, et al., 1999; Zhao, et al., 2004). Differences between the nasal cavities exceeding an order of magnitude may occur in olfactory region airflow volume while total respiratory volume remains approximately constant.

Semi-cyclical alterations in global airflow for each nasal cavity are commonly observed in humans and other mammals, with a time course of hours. These changes are known as the nasal cycle (e.g., Eccles, 1996). In the nasal cycle, reduction in airflow in one nasal cavity is often accompanied by a greater airflow in the other nasal cavity; total airflow may remain constant. The proximal mechanism for the reduced airflow appears to be localized and temporary enlargement of the nasal mucosa. Differences in orthonasal smelling are correlated with the airflow changes of the nasal cycle (Sobel et al., 1999). Sizeable alterations in local regional airflow of the olfactory regions, which can be expected to follow nasal cycle patterns, may underlie these differences in smelling. In addition, it is reasonable to suppose that trigeminal responses may be affected by nasal cycle differences in global airflow. However, relevant data are not available.

Vortices

Computational fluid dynamics has been used to numerically characterize air movement patterns in the nasal cavities. Streamline computational analyses of steady airflow find that vortices (rapid, swirling, spiral or spinning airflow around centers) may develop adjacent to both the nasal valve and the olfactory regions (Figure 1). This is of potential importance to smelling because " . . . vortices create air mixing and recirculation." (Zhao et al., 2004). For the olfactory region, these vortices may increase or decrease the airflow and odorant access. This may be partially due to the mixing effect of vortices and partially due to the airflow patterns, in which the direction of local airflow differs from that of the general airflow.

Physiological nasal respiration is characterized by changing airflow velocities within each inspiration and expiration (Ishikawa, et al. 2006). Graphic visualization of the three-dimensional aspects (Figure 3) of these orthonasal and retronasal airflow patterns was done using colors (Figure 4) to represent the computational fluid dynamics-derived velocities (Figure 4, m/s) and degrees of vorticity (Figure 4, 1/s). These patterns indicated that the locations of

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continued

maximum velocity in the nasal cavity, and the associated probabilities of vortex formation (vorticity), differed between inspiration and expiration (Ishikawa, et al. 2006). Specifically, at the time of maximum overall airflow velocity, orthonasal airflow (Ins) reached a greater localized magnitude than retronasal airflow (Exp), and the regions of the nasal mucosa that received the highest velocity and greatest vortex formation were not congruent for inspirations (Ins) and expirations (Exp) (Figure 4). Because location of trigeminal stimulation within the nasal cavity, corresponding to orthonasal or retronasal stimulus presentation locations, has been reported to alter the magnitude of both chemosomatosensory event-related potentials and perceived intensity (Frasnelli et al., 2004), the computed differences in localized maximum velocity (Figure 4) could be expected to alter not only retronasal but also orthonasal smelling.

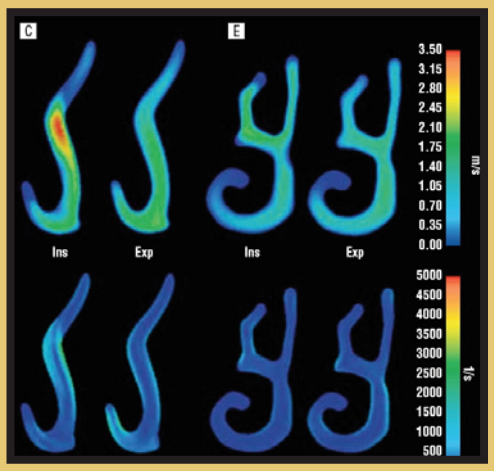

Figure 4. Velocity and vorticity (amount of rotation in the airflow) contour plots derived from numerical simulations (computational fluid dynamics) of inspiratory (Ins) and expiratory (Exp) nasal airflow velocity (m/s) and vortex formation (1/s) at the time of mid-inspiratory and expiratory phases (corresponding to maximum velocities) at two nasal cavity planes: the anterior portion of the interior turbinate (C) and mid-portion of the middle turbinate (E) (see Figure 3) of the right nasal cavity. For these simulations, respiration at rest (quiet breathing), with a tidal volume of 500 ml, and inspiratory and expiratory phase durations of 2.5 seconds (0.1 seconds resting phase), were assumed. It can be seen that inspiration and expiration differ in location of greatest velocity and vorticity. That is, maximum velocity and vortex formation were along the anterior portion of the middle turbinate during inspiration, but near the nasal wall during expiration. Reproduced from Ishikawa, S., Nakayama, T., Watanabe, M. and Matsuzawa, T. (2006). Visualization of flow resistance in physiological nasal respiration. analysis of velocity and vorticities using numerical simulation. *Arch Otolaryngol Head Neck Surg*. 132: 1203-1209, Figure 9, with permission of the American Medical Association. *Copyright © (2006) American Medical Association*. All Rights reserved.

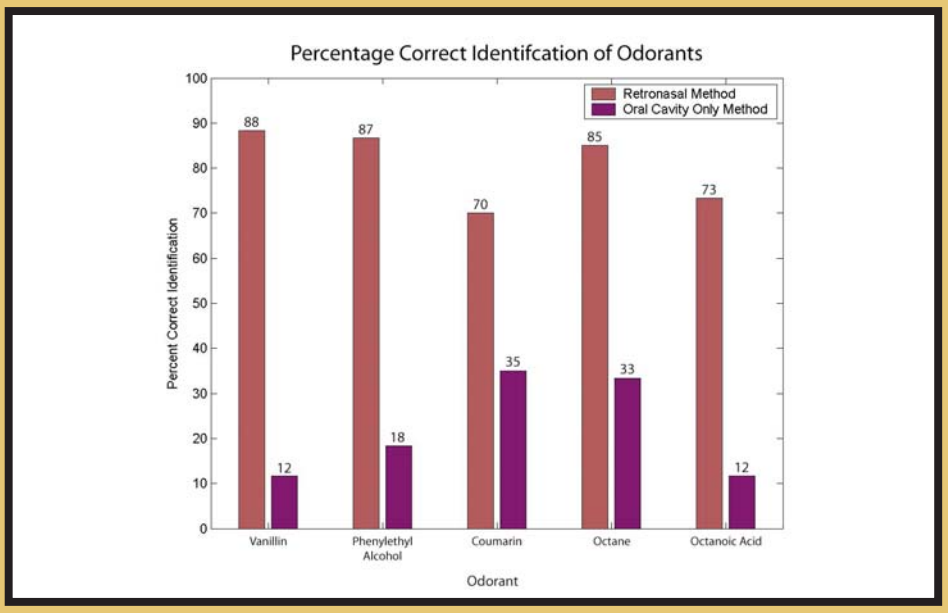

Figure 5. Overall percent correct identifications by 20 participants presented each of 5 air-phase odorants 3 times, randomized in blocks of 5, either retronasally (red bars) or oral-cavity-only (blue bars). Based on data in Chen and Halpern, 2008, Table 3.

Odorant distributions

Investigations with a variety of techniques have found direct evidence, albeit largely non-human, that under constant nasal cavity conditions the physicochemical characteristics of odorants, together with the airflow parameters, determine how much odorant, if any, arrives at various zones of the olfactory mucosa (Hornung, 2006). The same factors presumably affect the odorant concentrations available for trigeminal stimulation at some loci within the nasal cavities. Computational approaches confirmed these effects of different odorants and airflow parameters (Zhao et al., 2004). Computed whole nasal cavity mucosal odorant uptake was primarily determined by the physicochemical characteristics of odorants (90% uptake for methanol, 72% for L-carvone, 22% for d-limonene), with diameter of the nasal valve region having little or no effect (see Zhao et al., 2004's Figure 11A). In contrast, local olfactory region computed odorant uptake for the highly mucous-soluble and air-diffusible methanol decreased by more than two orders of magnitude when the nasal valve region was narrowed (see Zhao et al., 2004's Figure 11B). L-carvone local olfactory region uptake decreased by about an order of magnitude for the same narrowing, while much less change was computed for the low-mucous-soluble d-limonene. "This observation suggests that uptake of odorants with higher mucosal solubility and/or higher air diffusivity is more affected by local air flow pattern and anatomical changes than odorants with lower mucosal solubility and/or lower air diffusivity." (Zhao et al., 2004).

PSYCHOPHYSICAL RESPONSES

General considerations

Retronasal smelling thresholds for vapor phase odorants are generally higher than orthonasal thresholds (Voirol and Daget, 1986), even when equal concentrations of odorants are directly delivered to a nasal cavity before and after the olfactory region (Heilmann and Hummel, 2004; Halpern, 2004). However, as is discussed below, in natural breathing the complexities of airflow in the olfactory regions of the nasal cavities,

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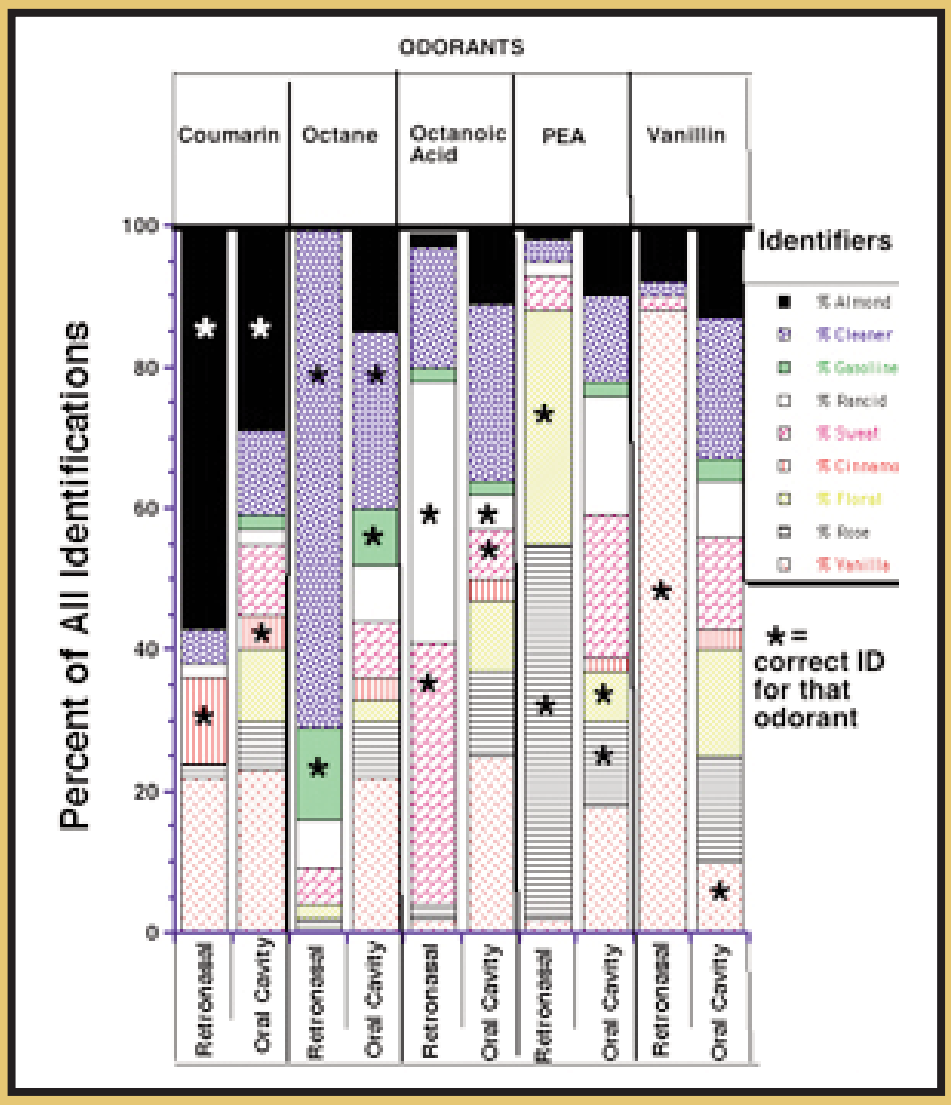

Figure 6. Percent identification across 20 participants for 3 trials of 5 air-phase odorants, randomized in blocks of 5, presented retronasally and oral-cavity-only. On each trial participants used a digital computer to select from a closed list of 9 identifiers. Based on data in Chen and Halpern, 2008's Table 3.

and entrance of odorants into the olfactory clefts (see Biacabe et al., 2004; Leopold, 1988), could nonetheless produce differences for odorant access during inspiration versus expiration, and thus for orthonasal versus retronasal smelling (Zhao, et al., 2005; Ishikawa et al., 2006; Pfaar, et al., 2006; Halpern, 2008).

Consistent, and unique to each vapor phase odorant, identifications of odorants during orthonasal smelling are often at a higher rate than during retronasal smelling (Halpern, 2004). However, when pairs of non-homogeneous (i.e., different) odorants are presented retronasally and orthonasally during natural breathing, identifications of orthonasally odorants are impaired more than retronasal identifications (Sun and Halpern, 2005). This difference presumably reflects central nervous system interactions (see Small and Prescott, 2005).

Sensory systems

Two sensory systems are available for human perceptual responses to vapor phase stimuli that travel through the nasal and oral cavities during respiration: the olfactory system and the trigeminal system (Halpern, 2008). Both of these sensory systems are present in the nasal cavities, but the olfactory system is absent from the oral cavity, including the oropharynx. Retronasal smelling would normally begin with odorants in the oral cavity during an expiratory phase of respiration. Therefore, the possibility exists for responses to vapor phase trigeminal stimuli to occur in the oral cavity prior to the arrival of the stimuli at the olfactory and trigeminal receptor arrays of the nasal cavities. Of course, for "purely olfactory" stimuli, origin in the oral cavity will generally not provide sufficient sensory input for identifications (Chen and Halpern, 2008).

The degree to which stimuli could be smelled when restricted to the oral cavity during expiration has been explored in several recent experiments. A necessary first step would have been to discover potential trigeminal vapor phase stimuli. This had already been done for orthonasal smelling and the nasal cavities with measures such as responsiveness by anosmics (Cometto- Muñiz et al. 1998, 2001, 2004, 2005; Doty et al., 1978) and lateralization without sniffing by normosmics (Cain et al. 2006; Frasnelli and Hummel, 2005; Hummel et al., 2003; Wysocki and Wise, 2004). Subsets of these stimuli, together with odorants that are thought to be non-trigeminal, were used in the following retronasal studies.

Recent studies

One study used natural extracts, some containing known trigeminal stimuli, to i) investigate whether previously known orthonasal identifications would also be selected as retronasal identifications, ii) compare retronasal and oral-cavity-only identifications, and iii) evaluate oral-cavity-only discriminability of the odorants (Dragich and Halpern, 2008). Retronasal correct identifications for vapor phase anise, cinnamon, coffee, orange (contains limonene), peppermint (contains menthol), and strawberry extracts were 88%, 81%, 98%, 95%, 91%, and 83%, and corresponded to typical orthonasal identifications. Five of the six could not be identified when restricted to the oral cavity, but vapor phase peppermint was identified above chance, albeit at only 33% correct. Next, ability to discriminate the six vapor phase odorants from their solvents when restricted to the oral cavity was tested. Across participants, the two extracts with known trigeminal components, orange and peppermint, were discriminated, plus,

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continued

surprisingly, strawberry extract. However, one quarter of the participants could discriminate all the vapor phase odorant from their solvents in the oral cavity. These data demonstrated a qualitative similarity between retronasal and orthonasal identifications of odorants. They also indicated not only that an additional oral cavity component can be available for retronasal smelling but also suggested that for menthol-related odorants, oral cavity responses may be qualitatively similar to nasal cavity responses.

The Dragich and Halpern (2008) observation that vapor phase menthol-containing peppermint extract was identified as peppermint when restricted to the oral cavity, led to a study in which identifications of vapor phase pure-chemical trigeminal stimuli, including dl-menthol, were investigated (Parikh et al., 2007; Parikh, 2007). As previous studies had suggested, the retronasal identifications of these trigeminal stimuli corresponded to prior orthonasal correct identifications: eugenol100% correct, heptyl alcohol 67%, nonanal 58%, 1-octanol 71%, dl-menthol 100% and valeric acid, 67% correct. However, when restricted to the oral cavity, the median correct identifications were all 0%, except for dl-menthol, for which correct identification was 67%. This outcome, building on the Dragich and Halpern, 2008, data, indicated that many vapor-phase trigeminal odorants can be identified only when access to the nasal cavity occurs, but dl-menthol is an exception, and suggested that odorants similar in some way to dl-menthol may contribute to flavor from both the oral and nasal cavities.

Although a range of trigeminal stimuli had been found to elicit retronasal identifications that were qualitatively similar to orthonasal identifications (Parikh et al., 2007; Parikh, 2007), the nature of retronasal identifications of odorants that appeared to have no trigeminal component, and therefore were considered 'purely olfactory', was unknown. This was of particular interest for two reasons. First, some vapor phase stimuli had already been found to be identifiable in the oral cavity, and more were discriminable. This suggested that an oral cavity component might usually be included in retronasal smelling. Removal of this component might disrupt retronasal identifications. Second, the trigeminal sensory array of the oral cavity might differ sufficiently from that of the nasal cavities to respond selectively to the so-called non-trigeminal odorants.

Prior studies had identified orthonasal vapor phase stimuli to which anosmics usually could not respond but normosmics could (Cain et al. 2006; Cometto-Muñiz et al. 1998, 2001, 2004, 2005; Doty et al., 1978; Frasnelli and Hummel, 2005; Hummel et al., 2003; Wysocki and Wise, 2004). These orthonasal "purely olfactory" odorants were used by Chen and Halpern (2008) to investigate retronasal and oral-cavity-only responses. Three questions were examined: i) Would consistent identifications be selected for these "purely olfactory" odorants when presented retronasally, ii) If so, would the identifications be similar to those that had been reported for orthonasal presentations, and iii) Would consistent identifications be selected for these "purely olfactory" odorants when restricted to the oral cavity?

It was found that, across participants and odorants, retronasal identifications of each "purely olfactory" odorant were very consistent (Figure 5), differed from those for the other odorants (Figure 6), and were similar to the orthonasal identifications that had been reported by other researchers. In contrast, the oral-cavity-only identifications were inconsistent (Figure 5) and did not differ from each other (Figure 6). These data indicated that for this set of odorants the oral cavity trigeminal system could not provide sufficient sensory information for consistent identifications (Chen and Halpern, 2008). Because of this, together with the positive retronasal outcome, it was implied, although not directly demonstrated, that the olfactory receptors of the nasal cavity, approached by a retronasal route, were the necessary and sufficient sensory components (Chen and Halpern, 2008). Moreover, as had been observed in other studies (e.g., Dragich and Halpern, 2008; Parikh et al., 2007), the retronasal identifications were qualitatively similar to orthonasal-based descriptions from prior research.

SUMMARY

Retronasal smelling, which normally occurs during expirations, has a major role in flavor. The nasal cavity olfactory and trigeminal receptor arrays are, in principle, accessible to odorant delivery during both expiration-dependent retronasal smelling and inspiration-dependent orthonasal smelling. However, because retronasal smelling normally starts in the oral cavity, it might begin with oral cavity trigeminal stimulation.

Airflow patterns within the nasal cavity have been modeled using computational fluid dynamic techniques, based upon CT scans of nasal cavities. These airflow patterns differ between inspiration and expiration, are strongly affected by the dimensions of the nasal valve region, and influence access of odorants to both the olfactory region and to mucosa innervated only by trigeminal nerve endings. The airflow factors interact with the mucous-soluble and air-diffusible properties of odorants, resulting in computed airflow patterns and odorant distributions for the nasal cavity that differ between retronasal and orthonasal smelling and vary with the physicochemical characteristics of odorants.

A series of psychophysical investigations of odorant identifications found that retronasal identifications of vapor phase natural extracts, of purely olfactory odorants, and of trigeminal stimuli, were qualitatively similar to prior orthonasal identifications. These data indicate that the differences between retronasal and orthonasal airflow patterns and odorant distributions do not preclude qualitative perceptual similarity. When the same odorants were restricted to the oral cavity, only peppermint extract, or dl-menthol, the major odorant in peppermint, were identified. However, in addition to peppermint extract, orange and strawberry extracts were also discriminated by all participants, and many extracts by about one-quarter of participants. These oral-cavity-only responses, for which the trigeminal sensory system is the only available sensory system, suggest that retronasal smelling may often have a trigeminal component that is not available to orthonasal smelling.

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continued

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WineSense:

Sweeter Tasting Wine Heralds Climate Change

Global climate change might bring a final high point to the quality of traditional styles of wine grown in France, before the it is transformed into a region growing "post classic wines" says viticulturist Richard Smart in *The Wine Industry Journal* (March-April) 2008, **23** (2), 85-88.

As higher average temperatures overtake the world's most famous wine regions, new wine styles will be produced in them, such as Petit Verdot, Carmeniere and Malbec. In Australia and elsewhere we should see more investment in grapevine breeding research to meet a hotter, drier climate.

Smart reports on the *Second International Climate Change Conference* and Wine Conference held recently in Barcelona. "If any attendee were in doubt about climate change, this conference would have changed their mind", he said.

Winemakers Michel Roland and Bruno Prats said wines from the Bordeaux region had become naturally higher in sugar content over the past two decades, this being in clear contrast to colder decades prior to 1973. The result is likely to be a period in which wines from Bordeaux are better than they have ever been: a golden age, followed by a decline and a need to make radical adjustments to what is grown and how increasingly scarce water is delivered to the vines.

Greg Jones, from Oregon University, reported that 27 of the world's wine growing regions have warmed by an average of 1.3ºC. The decline in the number of days below freezing and an increase in the number of frost free days, are amongst several indices of global warming, relevant to the wine industry.

As the world heats up, we are likely to see countries at higher latitudes enter the wine industry: such as Holland, Denmark and northern China. Smart's message to the conference was to plan for adaptation. He predicted that Southern Hemisphere countries will be less affected by climate change than those in the Northern Hemisphere, due to differences in landmass, with south west Australia, Tasmania, New Zealand, Chile and Argentina being least affected.

Al Gore attended the meeting in virtual form, by using a live interactive video link. People in the audience could ask him questions, so it was a "sustainable" and generally satisfactory way of including the former US Presidential candidate and Nobel Prize winner. Gore praised the wine industry for attempting to cut back on dependence on fossil fuels and for providing a good example to other industries, globally. He advises the industry to increase use of solar power for energy, to eliminate wastage and to increase efficiencies.

The conference also paid attention to how improvements in wine packaging might better serve a sustainable future, with the 300 year old technology of the glass bottle coming under scrutiny, as well as transport costs of goods to the winery and cased wine from it.

Smart concluded that "there are many opportunities for the Australian wine sector to adapt to climate change, and there is time to do it. A grapevine breeding program is needed to produce varieties for hot climates." ■

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21-25 July 2008	**International Symposium on Olfaction and Taste (ISOT) and AChemS Meeting** Hyatt Regency Hotel at the Embarcadero San Francisco, California, USA Abstract Deadline: 2 April, 2008 Early Bird Registration deadline: 15 April, 2008 Registration deadline 20 June, 2008 http://www.ISOT2008.org
17-21 August 2008	**The Chemical Senses and Health** Symposium Commemorating 100th Anniversary of ACS-AGFD and 40th Anniversary of Monell Chemical Senses Center. To be held during the ACS National Meeting, Philadelphia, USA Contacts: bachmanov@monell.org; beauchamp@monell.org; Lleland@kraft.com
3-7 September 2008	**18th European Chemoreception Research Conference (ECRO-2008)** Portoroz, Slovenia. http://www.ecro-2008.si
8-10 October 2008	**The 3rd IWA Specialist Conference on Odours and VOC** Barcelona, Spain Contact: r.steutz@unsw.edu.au
4-6 December 2008	**Australasian Association for ChemoSensory Science (AACSS)** Annual Scientific Meeting Griffith University, Brisbane Contact: j.reinhard@uq.edu.au ■

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