Chem. Senses 26: 1211–1219, 2001

Observation of the Swallowing Process by Application of Videofluoroscopy and Real-time Magnetic Resonance Imaging—Consequences for Retronasal Aroma Stimulation

Andrea Buettner, Ambros Beer, Christian Hannig and Marcus Settles

Deutsche Forschungsanstalt für Lebensmittelchemie, Lichtenbergstraße 4, D-85748 Garching and Institut für Röntgendiagnostik, Technische Universität München, Ismaninger Straße 22, 81675 München, Germany

Correspondence to be sent to: Andrea Buettner, Deutsche Forschungsanstalt für Lebensmittelchemie, Lichtenbergstraße 4, D-85748 Garching, Germany. e-mail: andrea.buettner@lrz.tum.de

Abstract

The process of eating and drinking was observed *in vivo* by application of videofluoroscopy, a dynamic X-ray technique, as well as real-time magnetic resonance imaging. The study was aimed at elucidating the timing and performance of the physiological organs involved in mastication and swallowing, mainly the tongue, the pharynx and the soft palate (velum palatinum). It was shown for the first time that effective physiological barriers do exist during food consumption that are capable of retaining volatiles such as helium within the oral cavity. These barriers allow the access of odorants to the nasal cavity only at certain times during the eating process. Their effectiveness is related to the texture of the food as well as the amount of food material present in the oral cavity and, thereby, directly influences retronasal aroma perception.

Introduction

In the last 20 years, numerous investigators have studied the temporal aspects of food consumption and their relationships to retronasal aroma perception. Time–intensity profiling has been developed, by which exhaled volatiles were monitored online using various mass spectrometric techniques (Overbosch, 1987; Soeting and Heidema, 1988; Lindinger *et al*., 1998; Taylor *et al*., 2000). Fitting the obtained release curves to functions representing the rise and decay of the curves, Overbosch developed a time-dependent form of the psychophysical function based on Stevens's law, thereby treating perception of taste and retronasal smell equally.

Recently, computer modelling was used to simulate the release of volatiles from liquid and solid foods in the mouth (Harrison and Hills, 1996; Harrison *et al*., 1998; Nahon *et al*., 2000). These models incorporated effects such as mass transfer of the volatiles across the solid–liquid and liquid–gas interfaces, heat transfer, saliva and air flow, mastication and swallowing (in terms of a withdrawing of food material and saliva from within the oral cavity). However, no prediction could be made on the timing and extent of an odorant's transfer to the nasal cavity, because no detailed information existed on the physiological constraints influencing this transport to include into the model, such as the nasal cavity's accessibility for odorants originating from the oral cavity. It has been implied that this transfer occurs during the tidal flows of breathing and that odorants are transferred from the oral cavity to the nasal cavity during exhalation, on condition that they have been released precedingly from food and saliva. The simulation of flavour release in systems modelling the mouth was also based on this assumption (van Ruth *et al*., 1994; Roberts and Acree, 1995).

Generally, the transport mechanism of odorants from the oral to the nasal cavity could not be fully explained. The oral cavity was regarded as a kind of cave, directly connected to the airways, allowing a free passage of odorants to the nasal cavity via the retronasal route. It was also assumed that 'the chewing motion causes the mouth to function as a bellows, injecting flavoured air into the exhaled air, which then passes the olfactory epithelium' (Haring, 1990), but this could never be proved by observation. Investigation of both orthonasal and retronasal odorant detection and identification, involving effects such as airflow, mucosa and sample presentation, supported the idea that both pathways (orthonasal and retronasal) lead to the same olfactory sensing system (Mozell, 1971; Voirol and Daget, 1986; Mozell *et al*., 1991; Hahn *et al*., 1994; Pierce and Halpern, 1996). Furthermore, it became evident that the efficiency in the delivery of odorants via either route depends greatly on the techniques used (breathing patterns, mouth and tongue movement conditions, etc.), so that different groups, comparing orthonasal and retronasal aroma intensities, gained

very divergent results. However, the physiological reasons for these disparities have not been elucidated.

In 1994, Land proposed that retronasal aroma stimulation was mainly related to the event of swallowing, when a small volume of air is exhaled immediately after swallowing, the so-called 'swallow-breath' (Land, 1994). He determined the volume of this pulse of air to be 5–15 ml with a soap-film flowmeter. It was assumed that this pulse should contain the major part of food volatiles that had been released from the food material prior to swallowing, and should therefore elicit a retronasal aroma pulse. Recently, we confirmed this theory by quantifying the exhaled amounts of odorants at time intervals during swallowing of liquid aroma solutions (Buettner and Schieberle, 2000).

Oropharyngeal deglutition is a complex process, activating 26 muscle groups within a very short period of time. Swallowing consists of three phases: (i) the preparation phase, which includes bolus uptake and chewing, and which is under voluntary control; (ii) the pharyngeal phase, which starts with the triggering of the swallowing reflex, lasts ~0.7 s and ends with the closure of the upper esophageal sphincter; and (iii) the esophageal phase, where the bolus is transported towards the stomach by primary and secondary peristalsis. A precise coordination is necessary to avoid aspiration or nasal penetration of the bolus, especially during the oropharyngeal phase of swallowing. Figure 1 is a schematic drawing showing the anatomy of the naso-, oro- and hypopharynx in the sagittal plane.

Oropharyngeal deglutition can be observed by real-time magnetic resonance imaging (MRI) as well as videofluoroscopy. Generally, the advantage of real-time MRI is the direct visualization of soft tissue, while soft tissue contrast in videofluoroscopy is unsatisfactory and a coating with barium is needed for good visualization of soft tissue surfaces. Another advantage of real-time MRI is the free choice of the image plane and the fact that no ionizing radiation is used. Videofluoroscopy, on the other hand, has superior temporal and spatial resolution, e.g. for analysis of dysfunctions of the upper esophageal sphincter. Another general limitation of MRI, unlike videofluoroscopy, is that examinations cannot be performed in an upright position, which is essential in patients with swallowing disorders or when there is a risk of aspiration. However, for analysis of the normal physiology of swallowing this seems to be of less importance, because once the swallowing reflex is triggered, the pharyngeal and esophageal stages of swallowing and bolus transport take place automatically and even against the force of gravitation. The transit time of a test bolus is slightly less in the tubular esophagus in a supine position than in the upright position [8.9 rather than 7.7 s (Hannig, 1995)]. Whether this is also true for the pharyngeal transit time has, to our knowledge, not yet been investigated. It is hard to quantify, because the pharyngeal stage of deglutition is very short (average duration = 0.7 s), as already mentioned above.

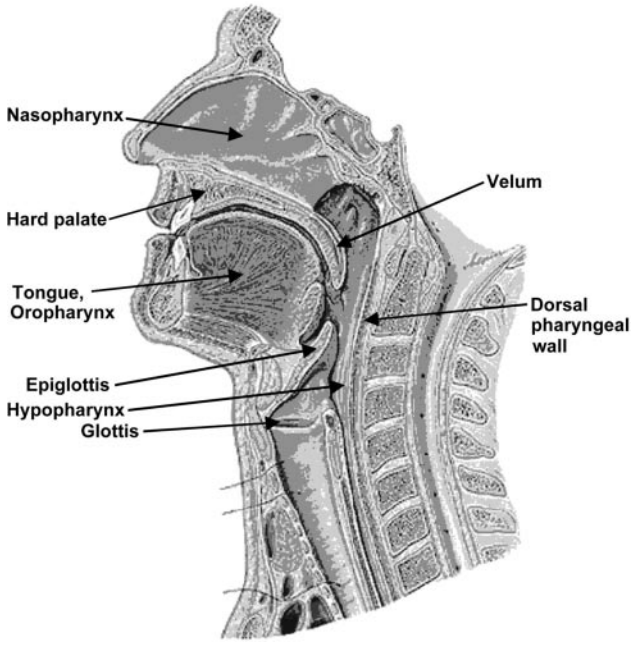

Figure 1 Schematic drawing of the naso-, oro- and hypopharynx in the sagittal plane [derived from (Putz and Pabst, 1998)].

To understand the physiological prerequisites of aroma transfer from the oral to the nasal cavity during retronasal perception, the present investigation is aimed at the observation of eating and drinking by videofluoroscopy and real-time MRI.

Materials and methods

Real-time MRI of swallowing

MRI was performed on a Philips Gyroscan ACS NT 1.5 T scanner (Philips, Best, The Netherlands). The gradient system had an amplitude of 23 mT/m in 0.2 s. We used a T1-weighted gradient echo sequence called a 'fast field echo'-sequence (T1-FFE). The repetition time was 3.2 ms, the echo time was 0.9 ms, the flip angle was 10°. Temporal resolution was 6 images/s and spatial resolution was 1.2 × 2.4 mm, with a slice thickness of 15 mm. A preparation of gadolinium-DTPA for oral use (magnevist-enteral®, Schering, Berlin, Germany) was diluted with tap water in a ratio of 1:4 and served as fluid contrast medium. As solid contrast medium, cookies coated with magnevist-enteral® were used.

Images were acquired in the sagittal and coronal plane during deglutition of fluid and solid contrast medium, respectively.

Videofluoroscopy

Videofluoroscopy was performed on a conventional fluoroscopy unit (Philips Diagnost 76) that is used mainly for examinations of the gastrointestinal tract (e.g. double-contrast studies of the colon or stomach). The unit consists

of an X-ray tube, an examination table for patient positioning and an image intensifier, which sends the images to a monitor. For videofluoroscopy, not only a monitor but also a videorecorder is connected to the image intensifier. Such a unit can be used in two different ways: (i) in the fluoroscopy mode, where a continous image is obtained, but with a very low dose and therefore a lower spatial resolution; and (ii) one can make still images or a series of images with up to 8 images/s with a higher dose, but also with a higher spatial resolution. The latter mode is used for making images of high diagnostic quality and for documentation on film. The average radiation dose for 1 min in the fluoroscopy mode is 3.13 mSv for the lung, 0.8 mSv for the thyroid gland and 0.54 mSv for the bone marrow (Biegenzahn and Denk, 1999). This is equivalent to one normal X-ray image of the same region of diagnostic quality. For the analysis of deglutition, a high temporal resolution is more important than a high spatial resolution; therefore, the images are acquired in the low-dose fluoroscopy mode and taped on conventional SVH-videotape for documentation and reporting. Temporal resolution was 25 images/s. Iotrolan (Isovist®, Schering, Berlin, Germany) served as fluid oral contrast medium. Cookies coated with Isovist® served as solid oral contrast medium. Images were acquired in the sagittal plane during swallowing.

Subjects

All subjects were non-pregnant volunteers of the Technical University of Munich. Five subjects participated in each experiment (two female, three male), and underwent both videofluoroscopy and real-time MRI. Written and informed consent was acquired from all volunteers. The subjects' ages ranged from 20 to 35 years. They exhibited no known illnesses at the time of examination. Also, there was no history of swallowing or eating disorders, or of oropharyngeal surgical interventions or radiation therapy in the past. During experiments, all of the participants exhibited normal olfactory and gustatory function. Subjective aroma perception was normal in the past and at the time of examination in all subjects.

The radiation dose for videofluoroscopy per minute for the radiation-sensitive organs exposed has already been mentioned. Average exposure time was 60 s for all four volunteers, with 30 s for the swallowing studies in the sagittal plane for the female volunteers and 90 s for swallowing studies with the additional helium test or studies for bolus uptake with a straw or spoon for the male volunteers. All volunteers wore a lead apron as protective clothing.

Chemicals

Helium gas (purity 4.6) was from Messer-Griesheim (Krefeld, Germany).

Helium transfer from the oral cavity to the nasal cavity

The experiments were carried out with helium gas as the 'ideal' gas: first, helium is a highly volatile gas and so it is readily transferred to the nasal cavity via the retronasal route as long as it is released from within the oral cavity; secondly, it does not exhibit any chemical interactions during its passage to the nasal cavity and so we can exclude losses; and thirdly, it can be easily detected in extremely small amounts in the air expired from the nose.

The experiments were carried out in the following ways: helium (25 ml) was taken into the mouth, with care being taken not to swallow. Subjects were asked to exhale through a nose-piece fitted exactly to the noses of the subjects so that the nostrils were completely sealed (Figure 2). The nosepiece was connected to a glass column and at the tip of the column a helium detector (GL 228, GL Sciences, detection limit: 0.01 ml/min) was positioned in the middle of the exhaled gas stream. The lips were kept closed throughout the entire experiment. The helium was kept for 1 min in the oral cavity while normal respiration was continued. Then, the air present in the oral cavity was deliberately exhaled through the nose. During the entire experiment the velum–pharyngeal performances were observed by means of videofluoroscopy. Experiments were carried out in duplicate. To make sure that retardation of helium indeed came from the velum–tongue border and not from helium collecting underneath the hard palate (due to its high volatility), the same experiments were repeated with the head bent down to the chest.

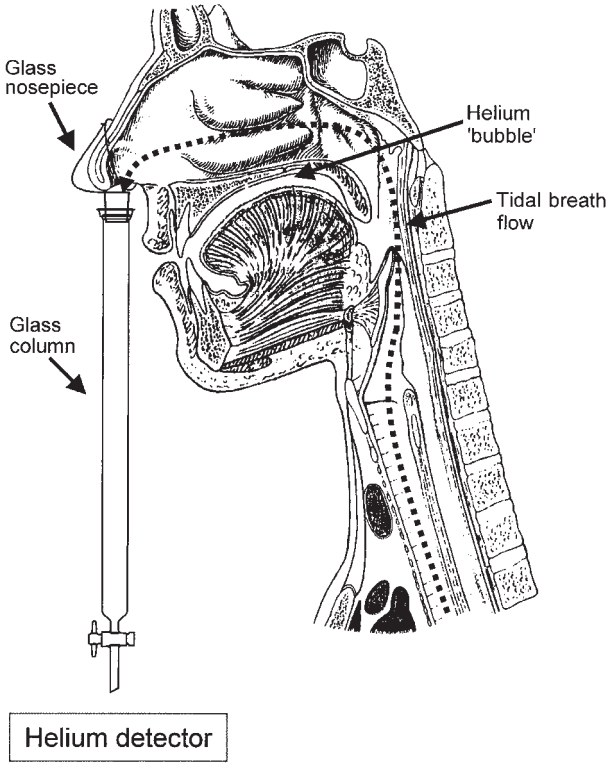

Figure 2 Glass device used for the detection of helium in expired air from the nose.

Results

Detection of helium in expired air from the nose—videofluoroscopic observation of the velum–pharyngeal performances

Observation of the oral and pharyngeal segments of a subject by means of videofluoroscopy was performed while the subject kept a 'bubble' of helium within the oral cavity (with closed lips and by avoiding any swallowing actions) (Figure 3a). Subjects reported that it did not require any effort to keep the bubble within the oral cavity. During this period, a barrier was formed by the velum and the base of the tongue that prevented the gas from passing the nasal cavity via the retronasal route and from being exhaled from the nose. As a consequence, no helium could be detected in the exhaled air. On the other hand, while performing a swallowing action (Figure 3b), a short opening of the velum–tongue border could be observed, along with an immediate detection of helium in the expired air from the nose. These observations were fully reproducible in every subject and at each repetition of the experiment. Even when the head was bent down to the chest, no transfer of helium to the nasal cavity could be observed as long as no swallowing action or deliberate opening of the velum–tongue border was performed. This clearly demonstrated that the closure of the velum and tongue is a highly efficient barrier even for extremely volatile and inert gases.

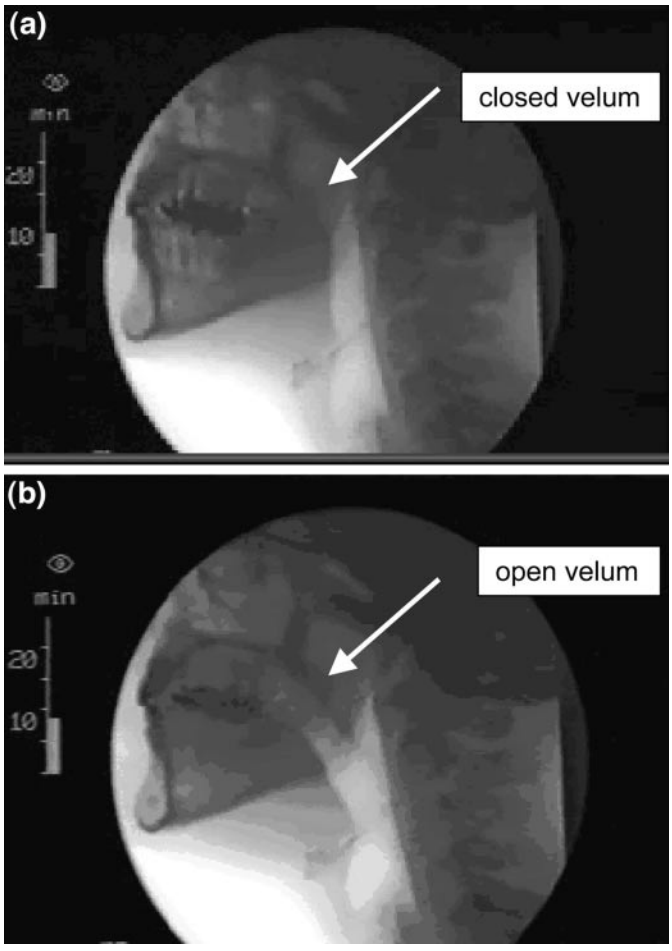

Figure 3 Observation of the oral and pharyngeal segments of a panelist by videofluoroscopy **(a)** during keeping a 'bubble' of helium within the oral cavity (closed velum) and **(b)** when performing a swallowing action (open velum).

Videofluoroscopy and real-time MRI of the swallowing of liquid foods

In Figure 4, the important oral and pharyngeal stages of swallowing are shown in six pictures from sagittal real-time MRI and videofluoroscopy series with fluid contrast medium. These stages of swallowing (bolus uptake, beginning of bolus transport, velopharyngeal closure, triggering of the swallowing reflex, propulsion of the bolus towards the esophagus, and original position) were selected according to Hannig (Hannig, 1995) and represent defined steps during the oral and pharyngeal phase of deglutition which have to be analyzed in the diagnosis of swallowing disorders.

After *bolus uptake*, the bolus is kept in the oral cavity between the tongue and the hard and soft palates. During rest, there is no connection to the dorsal oropharynx, the nasopharynx and the airways, preventing leakage and aspiration of fluids or solid material (Figure 4a). At the beginning of swallowing, we can observe an elevation of the tip of the tongue against the hard palate and an adduction of the soft palate to the base of the tongue (*beginning of bolus transport*, Figure 4b). During the next step, the soft palate performs a superior and posterior movement in order to achieve complete velopharyngeal closure to prevent nasal penetration while the bolus is transported to the hypopharynx (*velopharyngeal closure*, Figure 4c). Due to the anterior and superior movement of the larynx and closure of the epiglottis, the bolus cannot enter the airways and aspiration is prevented. At the same time, the contraction of the dorsal wall of the pharynx starts at the height of the first cervical vertebra, resulting in a propulsion of the bolus in the direction of the esophagus (*triggering of the swallowing reflex*, Figure 4d). In the next picture, the peristaltic wave of the dorsal pharyngeal wall continues and reaches the middle and lower parts of the pharynx, and the bolus enters the esophagus while the upper esophageal sphincter remains open (*propulsion of the bolus towards the esophagus*, Figure 4e). Finally, the bolus has left the pharynx, the upper esophageal sphincter is closed and the larynx, epiglottis and velum return to their original positions, followed by a short pulse of respiration, the so-called 'swallow breath' (Land, 1994) (Figure 4f). So, when swallowing liquids, a direct connection of 'odorant-loaded areas' to the nasal cavity, such as the oropharynx, exists only at the instant of the swallowing breath.

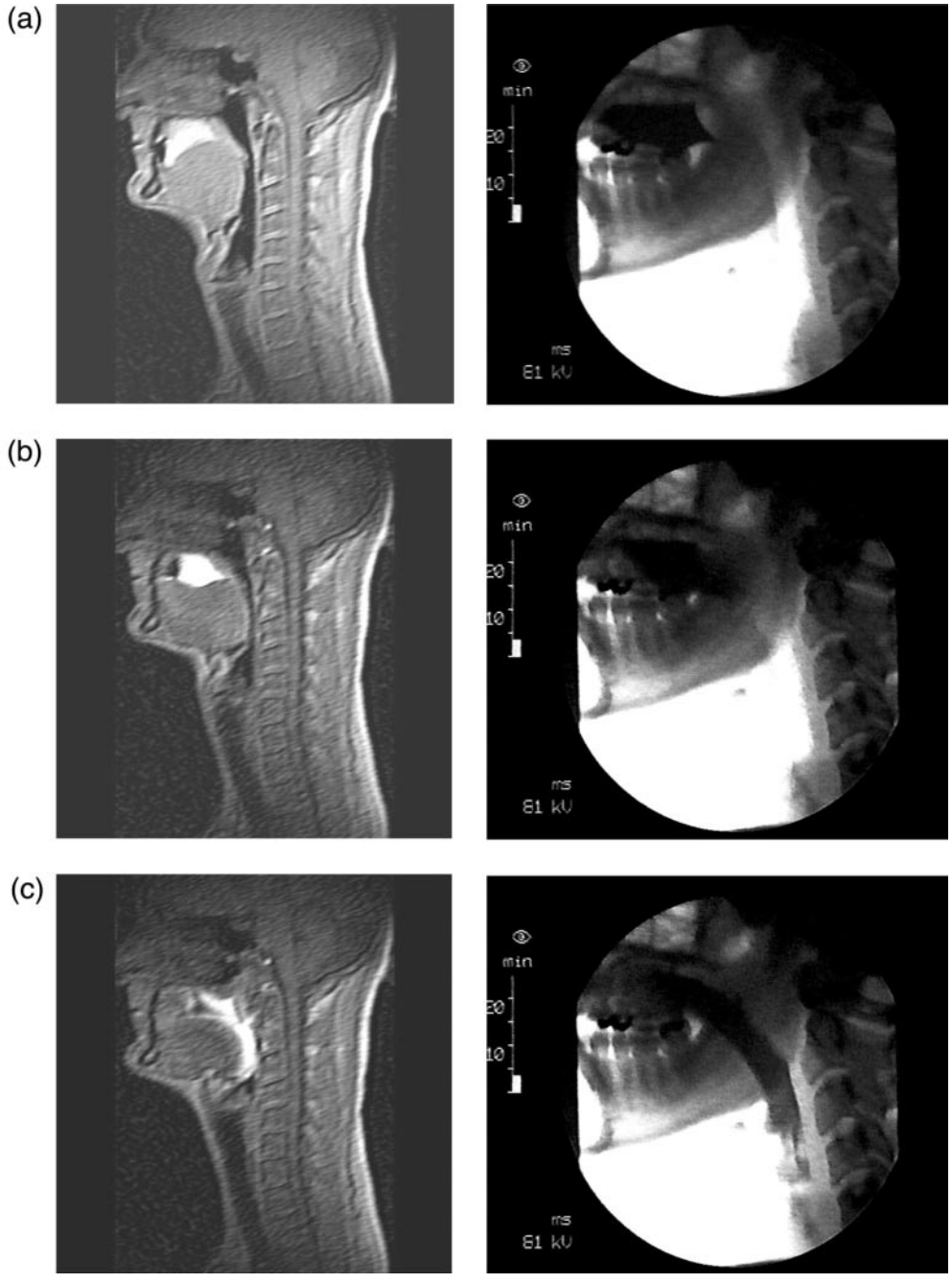

Figure 4 (a–c)

Videofluoroscopy and real-time MRI of the swallowing of solid foods

During mastication, intermittent opening of the connection of the oral cavity to the naso- and dorsal oropharynx can be observed, dependent on the texture and the amount of the bolus (Figure 5a, open oral cavity; Figure 5b, closed oral cavity). In general, the more fluid the texture of the bolus and the greater its volume, the more efficient is the closure of the oral cavity against the nasopharynx and dorsal oropharynx. During this closure no transfer of odorants is possible via the retronasal route to the nasal cavity and the olfactory epithelium.

Especially after swallowing solid or semi-solid foods, such as yogurt or cottage cheese, one can often observe the formation of a viscous salivary coating on the back (the pharyngeal part) of the tongue, which may contain particles of food along with odorants (Figure 6). This film could possibly induce a prolonged perception of food aroma, acting as a kind of odorant depot, while the main bolus has already left the oral cavity. This coating may still be

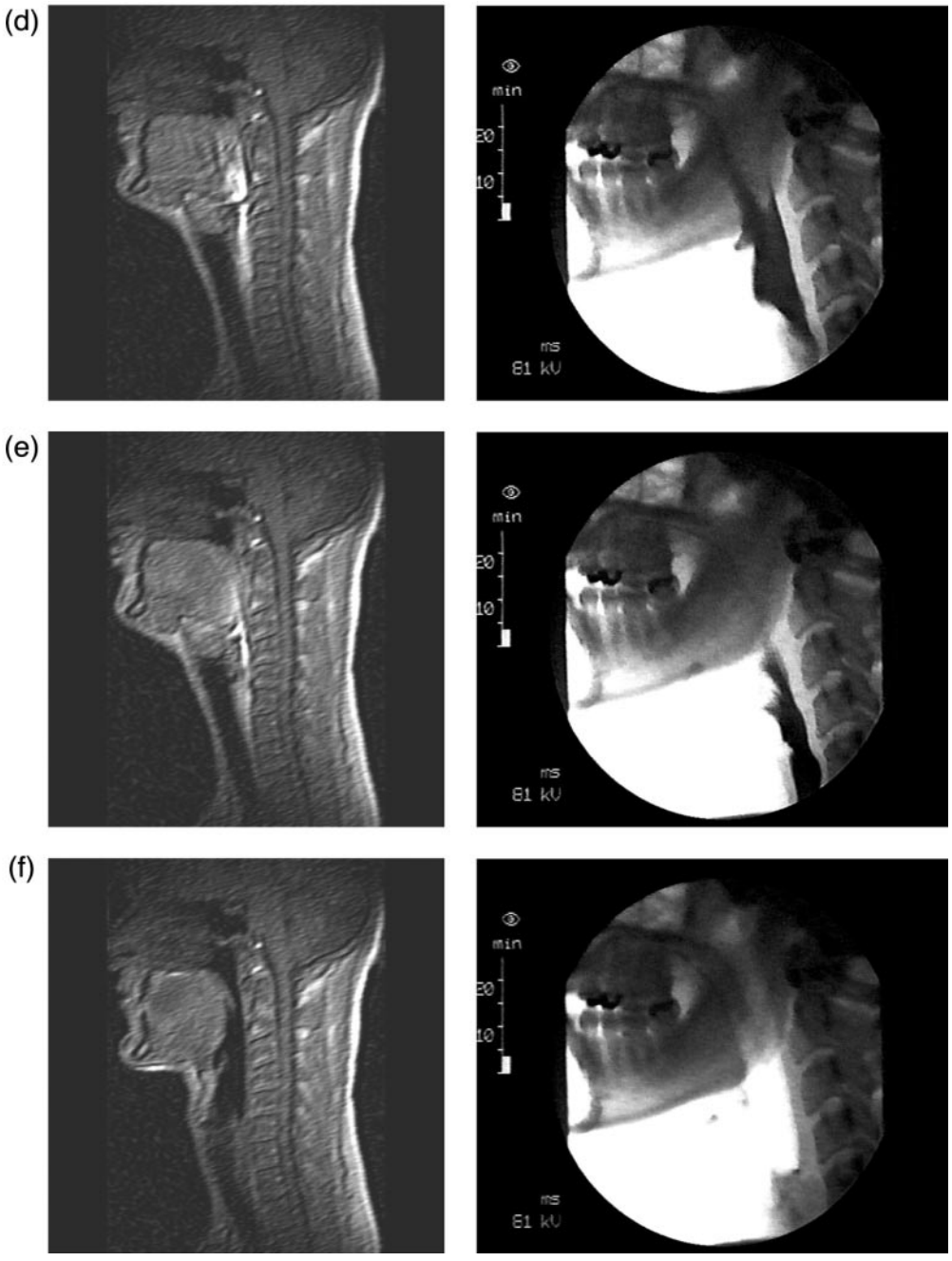

Figure 4 Six important oral and pharyngeal stages **(a–f)** of the swallowing of fluid contrast medium from a sagittal real-time MRI (left side) and videofluoroscopy (right side) series: (a) bolus uptake, (b) beginning of bolus transport, (c) velopharyngeal closure, (d) triggering of the swallowing reflex, (e) propulsion of the bolus towards the esophagus, (f) original position with swallow breath.

present even after another swallow of saliva, depending on the texture of the food matrix and its adhesion to the oral and pharyngeal mucosa.

The drinking of liquids by using a straw

There is an important difference in initial retronasal aroma perception between the conventional introduction of food (liquid and solid) and when using a straw.

During normal introduction of food into the oral cavity, the dorsal opening of the oral cavity (formed by the basis of the tongue and the soft palate) is open (Figure 7a), while when using a straw (Figure 7b), this region must be closed, otherwise no vacuum could be achieved. We suppose that when food material is introduced via the 'normal' way small portions of air can enter into the oral cavity along with the food and can proceed into the nasal cavity via the retronasal route through the velopharyngeal portal. For this reason, aroma perception is possible prior to chewing, whereas when

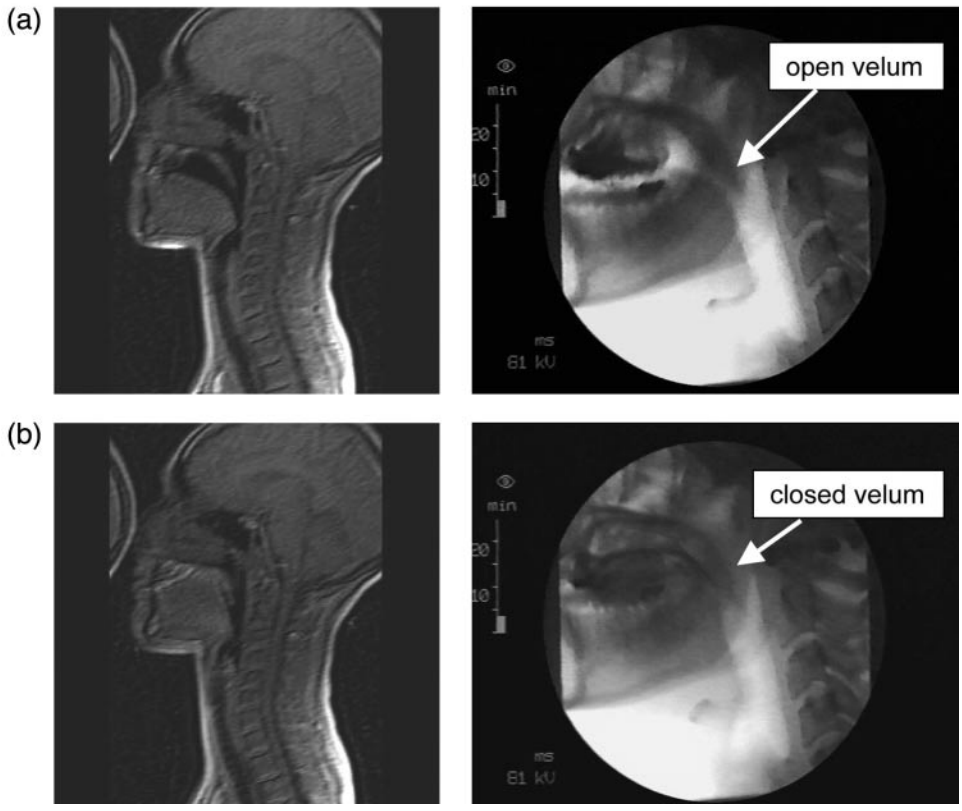

Figure 5 Observation of the mastication of solid material by use of a sagittal real-time MRI (left side) and videofluoroscopy (right side) series. **(a)** Open velum; **(b)** closed velum.

a straw is used, the perception of aroma is delayed, and is associated with the event of swallowing.

Discussion

Development of a new time–intensity concept based on velum–pharyngeal performances during the consumption of foods

The persistence of perception depends, first and foremost, on the duration of food material being present within the oral cavity. When swallowing liquid foods, retronasal aroma perception will be more or less reduced to one main aroma flash associated with the swallowing event itself. This main event will be followed subsequently by some minor events induced by the swallowing of some remaining traces of the liquid and by the delayed release of odorants from the oral mucosa. When masticating solid foods, there is a series of retronasal aroma perceptions, mainly related to the swallowing of small portions of the food material as well as portions of saliva. Generally, we found that the most compliant textures are swallowed first, e.g. liquids before solids. As a consequence, the odorants of the liquid phase are exhaled first. This can be easily observed when masticating e.g. a slice of orange (A. Buettner *et al.*, submitted for publication). With the first bites, considerable amounts of juice are present in the oral cavity which induce

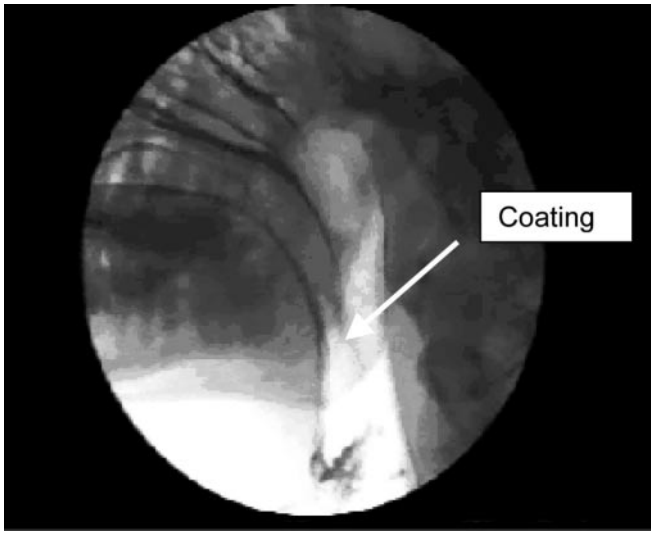

Figure 6 Formation of a viscous salivary coating on the pharyngeal part of the tongue after a swallow of semi-solid food.

the first swallowing actions. Evidently, the full body of the fruity juice aroma is perceived first, as long as juice is swallowed in portions. Later on, the pulp will be masticated and swallowed in portions. The eater will perceive a shift in the aroma profile, from fruity and fresh to a more terpene-like aroma, because the odorants associated with the pulp

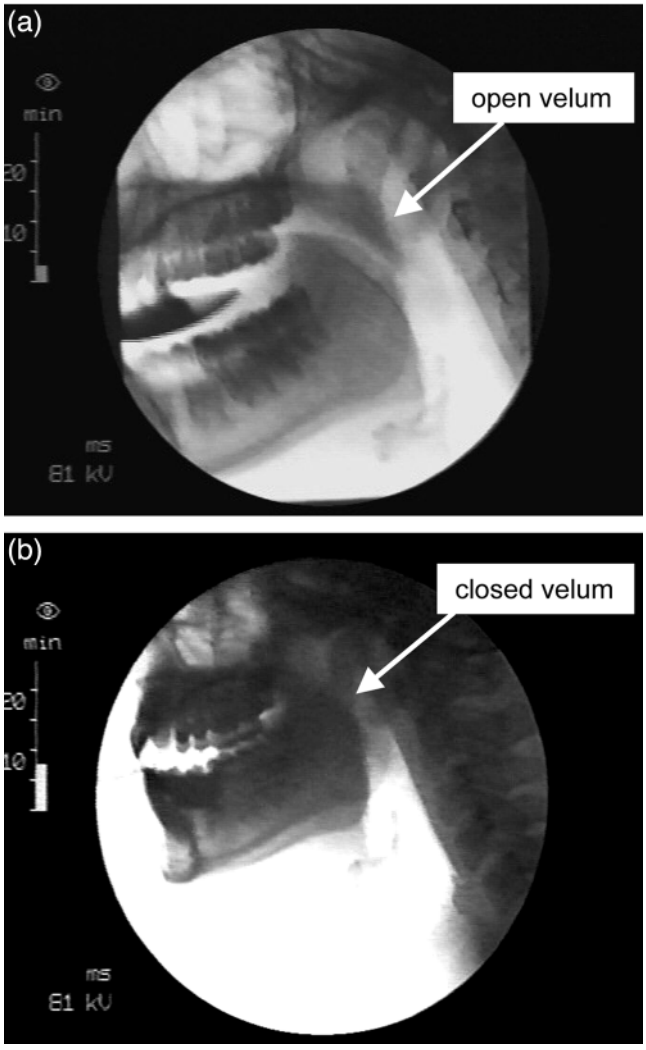

Figure 7 **(a)** 'Normal' introduction of food into the oral cavity by using a spoon: open velum; **(b)** introduction of food into the oral cavity using a straw: closed velum.

differ considerably from those in the juice (Radford *et al.*, 1974). The same effect can be observed when masticating a piece of bread with butter and jam. Small portions of jam and butter will be swallowed, together with saliva, at the very beginning of the mastication process, while the last overall impression will be dominated by bread aroma. As a consequence, the classical time–intensity (*TI*) curve with one single maximum of aroma intensity (I_{max}) cannot be maintained when we really want to evaluate the series of aroma impressions. We would, for heterogeneous food systems such as bread with butter and jam, have to separate into several I_{max}s, with each single I_{max} being related to one matrix constituent ($I_{max\text{-}jam}$, $I_{max\text{-}butter}$, $I_{max\text{-}bread}$). Even more complicated would be the occurrence of mix-phases as produced during mastication.

We propose that sensory time–intensity investigations, as performed up to now to follow the temporal dimension of aroma perception (Lee and Pangborn, 1986; Overbosch *et al.*, 1986; Overbosch and DeJong, 1989), need thorough reconsideration. In our opinion, perception of retronasal smell has to be regarded as a series of 'single-peak events' rather than a '*TI* curve', and should be carefully separated from the sensation of taste, temperature and the tactile feelings induced in the oral cavity during mastication. Particularly the sensations of temperature and taste should, indeed, exhibit a characteristic time–intensity profile, and it should be difficult to subtract these mentally from the series of single-peak events evoked by retronasal odorant perception. We suggest that this could be explored by very simple experiments: the subjects could, for example, place a portion of wine in their oral cavity and should first avoid swallowing actions. They should only perceive the coolness and the taste of the liquid. Then they could try to open the velum–tongue border deliberately, by (for example) inhaling small portions of air through the lips in addition to the liquid, but still avoiding any swallowing action. The more they succeed in performing such actions, the more retronasal aroma the panelists should perceive. Finally, they should evaluate the aroma impression induced by swallowing during the swallow breath.

According to our findings, it becomes evident why retronasal aroma perception can be considerably different from orthonasal sniffing. Mainly, when panelists are not aware of how to increase their retronasal perception either by swallowing or by deliberately opening the velum–tongue border, the perceived retronasal intensities will be significantly reduced. This phenomenon has been controversely discussed in previous investigations, effected by the sample evaluation technique (with or without swallowing), but could never be fully explained (Voirol and Daget, 1986; Marie *et al.*, 1987). The consequence therefore is highly variable retronasal aroma thresholds and intensity functions from different laboratories. Many of the difficulties reported previously in producing consistent sensory *TI* curves can now be easily explained.

Conclusions

Our investigations showed that aroma perception during drinking and eating depends highly on the velum–pharyngeal performances during mastication and swallowing. Aroma transport to the nose was found to be a series of alternating static and dynamic events such that the oral cavity can be either closed off from the airways by the borders formed by the velum or partially open to the nasal cavity depending on the oropharyngeal actions performed, such as swallowing. This depends strongly on the texture and the amount of food material present in the oral cavity, but also on the behaviour patterns during food consumption. Based on our novel physiological observations, a new approach to interpreting time–intensity data was proposed.

Acknowledgements

We are grateful to Mrs Pamela Gumbrecht and to Mr Daniel Schieberle for participating in our experiments and for excellent technical assistance.

References

Biegenzahn, W. and **Denk, D.M.** (1999) Oropharyngelae Dysphagien. Thieme Verlag, Stuttgart, pp. 46–47.

Buettner, A. and **Schieberle, P.** (2000) *Exhaled odorant measurement (EXOM)—a new approach to quantify the degree of in-mouth release of food aroma compounds*. Lebensm.-Wiss. Technol., 33, 553–559.

Hahn, I., Scherer, P.W. and **Mozell, M.M.** (1994) *A mass transport model of olfaction*. J. Theor. Biol., 167, 115–128.

Hannig, C. (1995) Radiologische Funktionsdiagnostik des Pharynx und Oesophagus. Springer-Verlag, Berlin.

Haring, P.G.M. (1990) *Flavour release: from product to perception*. In Bessiere, Y. and Thomas, A.F. (eds), 6th Weurman Symposium. Flavour Science and Technology. Wiley, Chichester, pp. 351–354.

Harrison, M. and **Hills, B.P.** (1996) *A mathematical model to describe flavour release from gelatine gels*. Int. J. Food Sci. Technol., 31, 167–176.

Harrison, M., Campbell, S. and **Hills, B.P.** (1998) *Computer simulation of flavor release from solid foods in the mouth*. J. Agric. Food Chem., 46, 2736–2743.

Land, D.G. (1994) *Perspectives on the effects of interactions on flavor perception: an overview*. In McGorrin, R.J. and Leland, J. (eds), ACS Symposium Series 633. Flavor–Food Interactions. ACS, Washington, DC, pp. 2–11.

Lee, W.E. and **Pangborn, R.M.** (1986) *Time–intensity: the temporal aspects of sensory perception*. Food Technol., 40, 71–78, 82.

Lindinger, W., Hansel, A. and **Jordan, A.** (1998) *Proton-transfer-reaction mass spectrometry (PTR-MS): on-line monitoring of volatile organic compounds at ppt-level*. Chem. Soc. Rev., 27, 347–354.

Marie, S., Land, D.G. and **Booth, D.A.** (1987) *Comparison of flavour perception by sniff and by mouth*. In Martens, M., Dalen, G.A. and Russwurm, H. (eds), Flavour Science and Technology. John Wiley & Sons, pp. 301–308.

Mozell, M.M. (1971) *The chemical senses. II. Olfaction*. In Kling, J.W. and Riggs, L.A. (eds), Experimental Psychology. Holt, Rinehart & Winston, New York, pp. 193–222.

Mozell, M.M., Kent, P.F., Scherer, P.W., Hornung, D.E. and **Murphy, S.J.** (1991) *Nasal airflow*. In Getchell, T.V., Bartoshuk, L.M., Doty, R.L. and Snow, J.B. (eds.), Smell and Taste in Health and Disease. Raven Press, New York, pp. 481–492.

Nahon, D.F., Harrison, M. and **Roozen, J.P.** (2000) *Modeling flavor release from aqueous sucrose solutions, using mass transfer and partition coefficients*. J. Agric. Food Chem., 48, 1278–1284.

Overbosch, P. (1987) *Flavour release and perception*. In Martens, M., Dalen, G.A. and Russwurm, H. (eds), Flavour Science and Technology. John Wiley & Sons, pp. 291–300.

Overbosch, P. and **DeJong, S.** (1989) *A theoretical model for perceived intensity in human taste and smell. II. Temporal integration and reaction times*. Physiol. Behav., 45, 607–613.

Overbosch, P., van den Enden, J.C. and **Keur, B.M.** (1986) *An improved method for measuring perceived intensity/time relationships in human taste and smell*. Chem. Senses, 11, 331–338.

Pierce, J. and **Halpern, B.P.** (1996) *Orthonasal and retronasal odorant identification based upon vapor phase input from common substances*. Chem. Senses, 21, 529–543.

Putz, R. and **Pabst, R.** (1998) Sobotta, Atlas der Anatomie des Menschen, 20th edn, cd rom version 1.5. Urban & Fischer, Munich.

Radford, T., Kawashima, K., Friedel, P.K., Pope, L.E. and **Gianturco, M.A.** (1974) *Distribution of volatile compounds between the pulp and serum of some fruit juices*. J. Agric. Food Chem., 22, 1066–1070.

Roberts, D. and **Acree, T.** (1995) *Simulation of retronasal aroma using a modified headspace technique: investigating the effects of saliva, temperature, shearing, and oil on flavor release*. J. Agric. Food Chem., 43, 2179–2186.

Soeting, W.J. and **Heidema, J.** (1988) *A mass spectrometric method for measuring flavour concentration/time profiles in human*. Chem. Senses, 13, 607–612.

Taylor, A.J., Linforth, R.S.T., Harvey, B.A. and **Blake, A.** (2000) *Atmospheric pressure chemical ionisation mass spectrometry for* in vivo *analysis of volatile flavour release*. Food Chem., 71, 327–338.

van Ruth, S.M., Roozen, J.P. and **Cozijnsen, J.L.** (1994) *Comparison of dynamic headspace mouth model systems for flavor release from rehydrated bell pepper cuttings*. In Maarse, H. and van der Heij, D.G. (eds), Trends in Flavour Research. Elsevier Science, Amsterdam, pp. 59–64.

Voirol, E. and **Daget, N.** (1986) *Comparative study of nasal and retronasal olfactory perception*. Lebensm.-Wiss. Technol., 19, 316–319.

Accepted August 30, 2001