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Chemical input – Sensory output: Diverse modes of physiology–flavour interaction

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ABSTRACT

Flavour perception is characterised by complex interactions between physicochemical processes (textural properties, aroma release, etc.) and (bio)chemical, physiological and behavioural phenomena. The complexity of 'peripheral' processes and their interaction and reciprocal feedback mechanisms is enormous and hitherto not fully understood. In this overview, diverse peripheral factors are discussed with a focus on behavioural responses to sensory stimulation during food consumption and the resulting feedback effects. This review thereby aims at deepening the understanding of a key issue: not only do the chemical structures and concentrations/compositions of food stimuli determine our sensory perception and appreciation of foods, e.g. in terms of flavour acceptance and preference, but specific behavioural and physiological parameters provide additional clues to understand how individuals perceive and respond to stimulations, e.g. acceptance or rejection.

1. Introduction

Despite the numerous studies and reviews that have hitherto focused on the many factors that influence flavour perception during eating (Piggot & Schaschke, 2001; Taylor, 1996; Taylor & Linforth, 1997), a series of investigations over the last 5–10 years has indicated that there is still a great lack of knowledge in our understanding of which sensations actually drive us to eat. This review article aims at providing an overview of current know-how on 'peripheral' factors influencing flavour perception during food consumption, focussing on volatile stimuli from foods. Selected parameters known to be of particular relevance until odorants reach the olfactory receptor site are discussed, with special attention given to the relationship between chemical, physiological and behavioural parameters, and processes that might influence one another via feedback and self-regulating mechanisms.

2. Peripheral factors that influence orthonasal perception

2.1. Breathing

The airflow patterns in the human nasal cavity were of interest quite early on in the search for understanding the basic principles of olfactory function (Scherer, Hahn, & Mozell, 1989). In order to characterise their underlying mechanisms, simulation models (both physical and virtual) were designed for tracing the pathways of odour molecules from the nares, via the olfactory epithelium, to the pharynx, and vice versa (Hahn, Scherer, & Mozell, 1993; Hornung, Leopold, et al., 1987; Keyhani, Scherer, & Mozell, 1995, 1997). In one such investigation, for example, anatomically correct 3-D models were established to study laminar and turbulent flow patterns in both 'orthonasal' and 'retronasal' modes (Hahn et al., 1993). Recently, studies based on computational fluid dynamics (CFD) techniques have even allowed the development of a 3-D nasal anatomy model that can predict airflow and odorant transport, specifically with regard to anatomical deviations such as polyps (Zhao, Scherer, Hajiloo, & Dalton, 2004). The authors found that variations in the nasal anatomy can play a different role during inhalation compared to during exhalation, which may provide a potential explanation, at least in part, of observed differences in olfactory sensitivity between orthonasal and retronasal sampling mode (Zhao et al., 2004). A similar modelling approach has been described by Ishikawa, Nakayama, Watanabe, and Matsuzawa (2006, 2009) in two recent publications investigating flow resistance in the nasal cavity and flow mechanisms along the human olfactory groove. In these papers, Ishikawa et al. (2006, 2009) visualise velocity gradients, vortices and the stream-line of nasal flow using a 3-D nasal and pharyngeal cavity model that was constructed from computed tomographic images of a healthy adult nose and pharynx. Concurrent with the Zhao et al. (2004) study,

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the Ishikawa et al. model found different flow patterns during inspiratory and expiratory breath phases, which they attributed to structural differences between anterior and posterior nasal components. Again, these effects may partly explain variations in orthonasal and retronasal olfactory perception.

In such studies, the degree of impairment of nasal airflow and olfactory ability is assessed by simulating the inspired and expired airflows using numerical finite volume methods. In particular, the effects of different breathing patterns and flow rates were investigated with regard to odorant delivery to the olfactory epithelium, which closely relates to early animal studies that revealed a strong relationship between odorant uptake, perception and localisation and sniffing strategies (Youngentob, Mozell, Sheehe, & Hornung, 1987). Such revelations provided an impetus for further attempts to elucidate specific smelling strategies in humans, via both experimental and modelling approaches. In a numerical model simulation, for example, Keyhani et al. (1997) demonstrated that an increase in nasal flow rate at a constant inlet concentration resulted in an increase in total olfactory uptake for all odorants. Furthermore, the authors showed that the odorant flux and fractional uptake in different regions of the olfactory mucosa is directly related to the polarity of the compound.

Recent studies by our group have shown that odorant delivery to the olfactory epithelium can be monitored as a function of odorant structure and is dependent on the breathing pattern involved (Beauchamp, Scheibe, Hummel, & Buettner, 2009). To achieve this, defined odorant stimulus delivery from an olfactometer instrument was coupled with parallel odorant monitoring directly at the olfactory cleft by proton-transfer-reaction mass spectrometry (PTR-MS) (cf. Fig. 1). Simultaneous monitoring of inspiration rate was also conducted via measurement of respiratory pressure variations. With this set-up it could be shown that odorant concentrations at the olfactory epithelium are strongly modified by the inhalation mode (normal breathing versus forced inhalation and sniffing).

These results indicate that studies involving odour intensity rating and evaluation of foods by panellists should take into account the specific inhalation techniques used for odorant delivery to the receptors, since regulation of this transfer is predominantly carried out unconsciously by the test subject. Restricted chewing and swallowing (and possibly even expectoration), as well as corresponding negative facial responses and grimaces, are well-known phenomena and responses for tastants (Delconte, Kelling, & Halpern, 1992; Steiner, 1979). Similarly, although barely investigated until now, there is a natural reaction of a person not to inhale in the same manner or with the same intensity when presented with a non-attractive odorant compared with exposure to a pleasant odour, which has been demonstrated even for imagined odours (Bensafi et al., 2003). Accordingly, the aforementioned approach (Beauchamp et al., 2009) can be used to: (a) directly monitor inhalation efficiency by measuring the inspired volume and flow as a response to a specific odour stimulus, and (b) characterise the extent of odorant delivery to the olfactory epithelium (cf. Fig. 2). As can be seen from Fig. 2, concentrations at the olfactory epithelium of 2,3-butanedione presented at the nostril decreased with increasing nasal air pressure (i.e. inspired volumes) from the three inhalation modes: normal nasal breathing; sniffing with intermittent stops (e.g. as performed by dogs searching out an odour source); and forced, deep inhalation. These results suggest that the act of 'sniffing' is indeed not the preferred inhalation mode by humans when trying to heighten their odour sensitivity. This assumption is supported by our findings that the majority of panellists reported highest intensity perception for normal inhalation of 2,3-butanedione, as has been similarly observed by Kleemann et al. (2009).

Using this approach, differences in odour transfer efficiencies, specifically from the odour source to the nasal epithelium, in relation to the inhalation of different odorants can be assessed for better comparability between substances. This could be achieved, for example, by mixing a solution containing both non-odorous and odorous marker substances and directly monitoring and comparing the responses to the individual appreciation of the stimulus. This method would overcome the problem of odorants exhibiting a temporal delay in their delivery to the olfactory epithelium as a result of their chemical specificities, such as polarity and molecular weight. Thus, variations in odorant transfer, for example due to constricted inhalation (e.g. when a negatively rated odorant is inhaled), can be specifically related to the marker substance and monitored in a quantitative and temporal assay.

2.2. Effects of nasal mucosal tissues

Early electrophysiological studies on bullfrogs by Mozell et al. monitored neuronal activity in the posterior and anterior regions

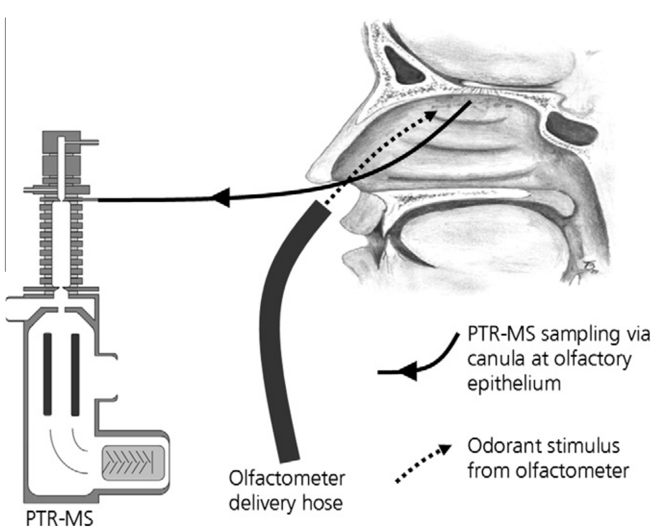

Fig. 1. Schematic depiction of the experimental set-up for determination of odorant transfer to the olfactory epithelium as a function of breathing pattern and odorant structure. Image adapted from Frasnelli et al. (2005).

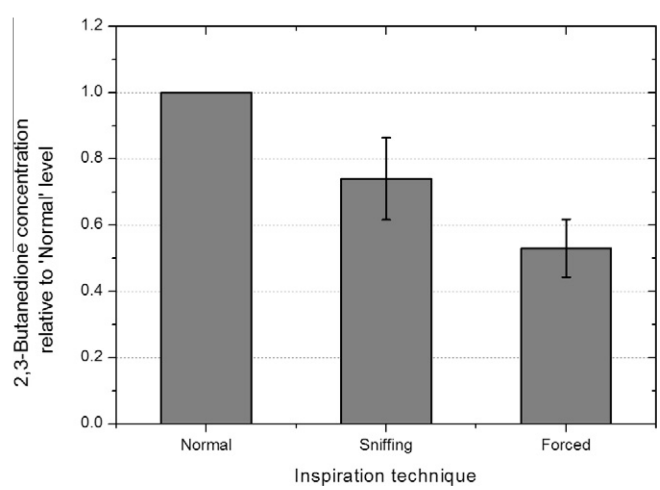

Fig. 2. Mean maximum intra-nasal odorant concentration of 2,3-butanedione directly at the olfactory epithelium (determined via on-line PTR-MS measurements; see text and Fig. 1) of 12 panellists as a function of inhalation technique (normal breathing, sniffing with repetitive irregular inhalations, and forced inhalation with deep breathing under high air flow). Data have been normalised to the 'normal' inhalation level of each panellist to smooth out inter-subject variations. The error bars represent the standard error on the mean. Data taken from Beauchamp et al. (2009).