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Chapter 8

FLAVOUR RELEASE AND SENSORY PERCEPTION IN CHEESES

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ABSTRACT

During the eating of food, the in-mouth process leads to food breakdown which induces the release of flavour compounds. Volatile and non-volatile compounds are released into the saliva, and volatile compounds are transferred into the vapour phase to reach olfactory receptors in the nasal cavity.

The aim of this chapter is to review the effects of changing the composition of cheeses on the mobility, release and perception of flavour molecules (salt, aroma compounds), and to discuss the results with respect to human physiology. Cheese is a good model because it is possible to vary its composition (in lipids, proteins, salt), in order to comply with nutritional guidelines (less salt, less fat) and to study the effects of these changes in composition on its microstructure and texture, and then on flavour (taste and aroma) release and perception, while taking account of in-mouth breakdown.

Papers on this subject have mainly been related to either salt release and perception or aroma release and perception, and few have taken account of the combined effects of cheese composition on both salt and aroma release and perception. Indeed, recent papers from our research group have shown that the salt and fat contents of cheeses induce modifications to texture and microstructure that affect not only salt release and perception but also aroma release and perception and chewing behaviour.

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INTRODUCTION

The acceptability of food by consumers is mainly due to sensory perception. Overall perception involves aroma, taste and texture, and the perception of aroma and taste cannot solely be explained by chemical composition but also by the interactions which occur at both a physicochemical level in the food matrix and a sensory level. Cheese is a complex food in terms of its composition and structure, and it contains a large number of aroma compounds that form naturally during manufacture. Understanding sensory perception in cheese needs to take account of the release of flavour stimuli, their interactions with the food matrix, perceptual interactions and oral physiology (Figure 1).

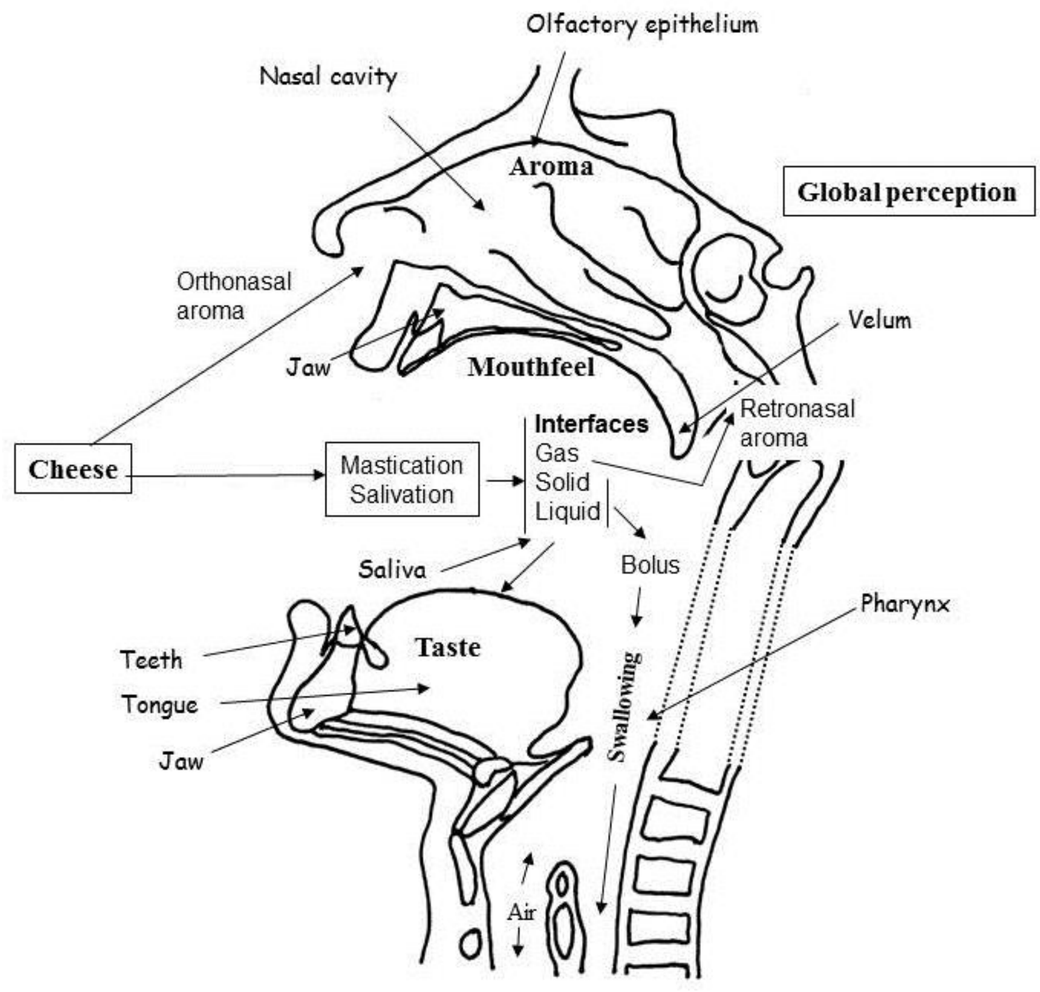

Figure 1. Principal events which occur in the mouth when eating cheese.

The aim of this chapter is therefore to discuss the relationships between the composition in odorant and taste molecules, their retention and release from cheese and their overall perception, including that of texture. Identification of the molecules responsible for cheese aroma will not be presented in this chapter. The first section focuses on the mobility and release of salt as a function of the composition and structure of different cheeses; the second section presents the different aroma compounds, their interactions with the cheese matrix and their release during consumption, and the final section concerns the effects of salt and aroma release on perception.

Taste Compound Release from Cheese Matrices

Taste is the sensory system that enables humans to check the quality of the food to be ingested [1]. Together with aroma perceptions and trigeminal sensations, it is an important sensory component of the overall flavour perception of food. Humans are able to discriminate at least five taste qualities: bitterness, sweetness, sourness, saltiness and umami. Taste buds are located on the tongue and all taste qualities can be elicited from all regions of the tongue. The taste buds contain numerous taste cells, and taste information linking chemical stimuli to taste perception is encoded by the nervous system where all sensory information is integrated to generate an overall flavour perception. Two types of process can be distinguished regarding taste receptors. Sourness and saltiness are due to ionic compounds detected by the ion channels, while umami, sweet and bitter perceptions imply the activation of receptors coupled with G proteins [2]. During the in-mouth process, tastants are dissolved in saliva, either directly by dilution in the case of liquids or progressively during the mastication of a solid food, after which they enter into contact with the taste cells. This interaction is the initial step in the taste perception process.

In the case of cheeses, the principal tastants are mineral salts, particularly sodium chloride, lactate and more generally organic acids, amino-acids, peptides, etc., which elicit a broad range of taste qualities. For example, the compounds responsible for the aroma and taste of camembert and goat cheeses were found in the water-soluble fraction of cheeses [3, 4]. This water-soluble fraction, which also contains a fraction of volatile compounds, is highly representative of a typical cheese flavour. Among the non-volatile taste compounds found in cheeses, most sodium chloride is added during the cheese-making process, mainly to ensure preservation and drainage, but its multifunctional nature is well known as it is also involved in structure, texture, crusting, ripening process and organoleptic properties. Moreover, sodium chloride is often found as a flavour enhancer. In model cheeses, for example, an increase in the salt content enables a higher intensity of overall aroma [5].

The spotlight has been thrown on salt in recent years because sodium-rich diets have been widely demonstrated as promoting hypertension, which is a risk factor associated with cardiovascular diseases [6]. The salt content in cheese can reach up to 6% of total weight and constitutes an important source of sodium intake [7]. So in order to reduce the risks of hypertension and its associated healthcare expenditure, many countries and health organisations have encouraged the food industry to reduce the salt content in processed foods [8, 9]. This section mainly focuses on this tastant, describing the mobility of sodium chloride at different levels, in-mouth sodium release during eating and saltiness perception.

Mobility and Movement of NaCl at the Microscopic and Macroscopic Levels

The release of salt from a food matrix into an aqueous phase can be studied dynamically by following salt diffusion during the process, or in a static manner, at equilibrium, via the water/matrix partition coefficient of salt.

Water/Matrix Partition Coefficient of Salt

Unlike aroma compounds, taste compounds such as sodium chloride are not soluble in lipids. In the mouth, these compounds are transported to the taste receptors through a continuous aqueous phase: saliva. This transport is more or less rapid depending on the compound being considered and the composition of the aqueous phase [10].

The partition properties of sodium chloride have been very little studied in the food field. To our knowledge, only two methods have been reported:

- A diffusion cell developed to determine the partition coefficient of sodium chloride between water and an agar gel [11]. This method was applied subsequently to cheese products [12].
- The solid/liquid – phase ratio variation (SL – PRV) developed on model cheeses [13, 14], which is an adaptation of the PRV method used for volatile compounds [15].
- The drawback of the second method is that the associated analytical technique (Conductometric detection) is not specific to sodium chloride. The lack of an effect of the fat or protein content in model cheeses on the partition coefficients of sodium chloride may be due to an absence of selectivity in this technique.

To study the water/food product partition in model cheeses, the soluble sodium concentration in the water phase, after centrifugation, can also be considered versus the total sodium concentration [16]. In this case, the sodium ion partition is higher when the fat/dry matter ratio, sodium chloride content and pH all increase. These effects have been explained by their effects on the microstructure of model cheeses.

Salt Diffusion and Release

In the case of real cheeses, the diffusion of salt from brine to the cheese has been studied extensively in attempts to explain the mechanisms in play. The second Fick law has been widely used for studies on the diffusion of sodium chloride during the salting or ripening steps [12, 17].

This law reflects the variation in concentration at a given point as a function of time, and is expressed as:

$$\frac{\partial c}{\partial t} = D_i \cdot \frac{\partial^2 C_i}{\partial x^2}$$

Where $\frac{\partial c}{\partial t}$ represents the variation in concentration as a function of time, *Di* is the diffusion coefficient and $\frac{\partial^2 C_i}{\partial x^2}$ represents the variation in concentration according to the *x* axis of diffusion.

The principal factors which influence salt diffusion into the cheese have been postulated [17] as being:

- the pore size of the cheese, which governs both sodium chloride diffusion and water reverse diffusion, the latter being about twice as much as sodium chloride diffusion,
- the apparent viscosity of the water phase of cheeses containing several dissolved minerals (acids, salts, nitrogen compounds), which limits sodium chloride diffusion,
- the tortuousness of the cheese matrix because of the obstructions caused by fat globules and protein particles, and
- the water that is bound to proteins, thus increasing the effective diameter of proteins and being responsible for friction effects.

These factors should be taken into account when determining an adjusted partition coefficient for sodium chloride [17]. Using such an adjusted coefficient, sodium chloride diffusion from the water phase to cheese increases when the dry matter content decreases and the fat ratio increases [18].

The diffusion of salt from a cheese matrix to a water phase has been studied less, although a concentration gradient is also at the origin of salt diffusion. However, some studies have focused on the effect of the composition of model cheeses on the diffusion of sodium chloride. One of the main factors affecting sodium chloride diffusion is the dry matter content of model cheeses. Indeed, a reduction of just 32% in the dry matter content can cause an 80% increase in the sodium chloride diffusion coefficient [19]. The same type of effect has also been reported regarding the diffusion of sodium chloride in artificial saliva [20]. This effect of dry matter can be explained by an increase in hardness, a reduction in the water available for the transport of sodium chloride and an increase in the sieving effect of the protein network. But the ingredients used to produce model cheeses can also influence the coefficient of sodium chloride diffusion, and it has been shown that this increases when the sodium chloride and fat contents of the model cheeses rise [19]. As for fat, the effect seems to be associated with a simultaneous reduction in the protein content, which facilitates the diffusion of NaCl. It has thus been shown that it is difficult to differentiate the effects of each constituent on sodium chloride diffusion because a variation in the content of a constituent will often modify that of another constituent.

It has been demonstrated that sodium and chloride ions from sodium chloride in the model cheeses diffuse in the same way as they do in water, because their release patterns could be superimposed [20]. This confirms that sodium or chloride ions are good markers for the study of sodium chloride release.

Mobility of Sodium at the Molecular Level: ^{23}Na NMR

NMR is the technique of choice for a variety of molecular studies. ^{1}H NMR allows study of the interactions between molecules, and particularly between aroma compounds and macromolecules [21]. Recent NMR developments have been applied to food studies [22]. In dairy products, the most commonly studied nuclei are ^{1}H, ^{13}C (mainly for fat), and ^{31}P (mainly for phosphorylated compounds such as phospholipids) [23]. The mobility of phosphate ions has been studied in cheeses using ^{31}P NMR [24].

Recommendations from the public health authorities to reduce salt intake have made it necessary to characterise and quantify the bound state and the content of sodium ions in foods. To achieve this, ^{23}Na NMR can be used to determine the content of bound and total sodium ions in food matrices, in a non-invasive manner [25, 26]. This technique can be used for both food and non-food applications. For example, it is used to study sodium dynamics in porous materials [27, 28], biopolymers [26] and biological tissues [29, 30], or to study sodium ion distribution in systems such as pectin gels [31], ion exchange resins [32] or iota-carrageenan systems [33], and also in foods such as salted pork meat [34], smoked salmon [35], cheese [24] or bread [36]. For such studies, the detection of all sodium ions has been validated by single quanta ^{23}Na NMR (SQ), while the bound sodium fraction can be studied using double quanta ^{23}Na NMR experiments (DQ). These ions are found in a specifically ordered environment, with lower mobility.

Competitive binding between KCl and NaCl has been shown in gum systems to modify salty perception [37]. Endogenous potassium and calcium ions, or added potassium chloride, will bind preferentially ionic gums, allowing a larger quantity of available sodium ions to elicit a salty perception. This phenomenon was revealed by the greater mobility of sodium ions following the addition of those referred to above. By contrast, in the case of caseins, the authors attributed a reduction in salty perception to the ability of sodium ions to bind caseins and consequently not to be involved in salty perception.

The results obtained using NMR have shown that this technique can satisfactorily quantify free and bound sodium ions. This is a determinant factor in the characterisation of salted food products. However, few studies have reported an absolute quantification of the bound sodium fraction using NMR spectroscopy. To date, absolute quantifications of sodium have only been performed on ion exchange resins [32], iota-carrageenan gels and cheeses [38] and, more recently, on bread [36].

NMR enables study of the interactions between sodium ions and the environing constituents at the molecular scale, which can be supplemented by studies at the microscopic and macroscopic levels in order to better understand the phenomenon of sodium release. A recent study reported the molecular mobility of sodium in cheeses as a function of their composition and structure determined by ^{23}Na NMR spectroscopy with both single quantum and double quantum filtered sequences [39]. Using model cheeses differing in terms of their lipid/protein ratios and salt levels, they notably observed that the mobility of sodium decreased when the hardness of these model cheeses increased. Sodium ions were less mobile when the protein content increased and the lipid content decreased. This could be explained by the weaker elasticity and greater resistance of model cheeses with a higher protein content and lower lipid content. For the same lipid/protein ratio, sodium ions were found to be less mobile in salted model cheeses, suggesting that this mobility might be linked to differences in microstructure and rheological properties. As for the bound sodium fraction, the bound sodium/total sodium ratio did not vary in line with product composition. The time required for sodium binding was shorter when the model cheese was firmer, due to a better organized system around the bound sodium (Figure 2). At the macroscopic level, the water-matrix partition coefficient of sodium, lower than 1, indicated that some sodium was retained in the cheese matrix, and decreased as the model cheese became firmer. These observations agreed with the results obtained at a molecular level and further demonstrated the value of ^{23}Na NMR as a powerful tool to quantify total and bound sodium.

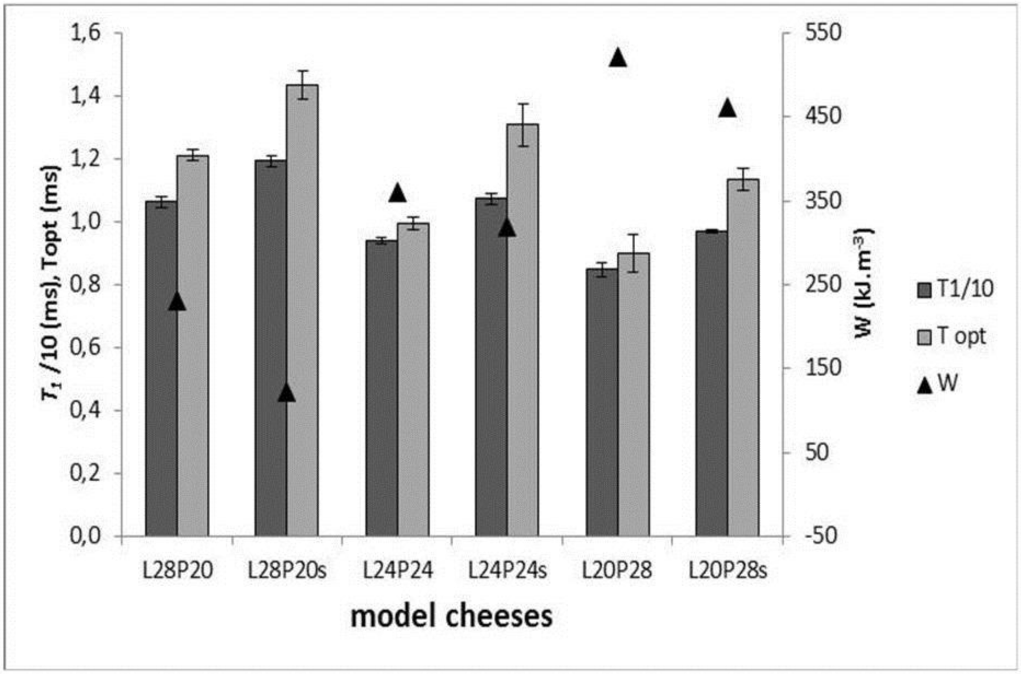

Figure 2. Sodium mobility measured using ^{23}Na NMR and represented by longitudinal relaxation time (T_1/10) and organization of the environment around "bound" sodium ions measured by the creation time (T_{opt}) as a function of cheese firmness determined by work to maximum deformation (W). Model cheeses vary in lipid (L)/protein (P) ratios and salt content (s means addition of salt).

In-Mouth Sodium Chloride Release during Consumption

This section concerns the effects of mastication and salivation on in-mouth sodium chloride release.

Effect of Saliva on Sodium Chloride Release

Saliva has numerous effects on mastication, swallowing and digestion [40, 41]. Saliva acts as a solvent for taste compounds and allows their access to taste receptors [42], but this access is dependent on the salivary flow rate [43-45]. In terms of its composition, it is known that salivary HCO_3^- ions participate in the buffer effect of this fluid so they may affect sourness perception [46]. Other saliva components such as amylase and lipase may also interfere with food components (e.g. starch, lipids) and be responsible for hydrolysis [42, 47]. During the eating of model cheeses, the salivary flow rate may influence sodium chloride release. At a low flow rate, salt is extracted more slowly [48], and to a lesser extent [49] from a model cheese during mastication. Saliva contains sodium and chloride ions and their concentration at rest is sufficient to stimulate salty sensory receptors. However, we only perceive the concentration higher than those the taste receptors are adapted [50].

Effect of Mastication on Sodium Chloride Release

In-mouth taste perception is a dynamic process [51]. Consequently, in-mouth salt release needs to be studied at different time points during consumption. The quantity of non-volatile compounds released into saliva generally increases at the start of the mastication, peaks and then declines towards the end of mastication [52], this peak often being reached during the first minute of mastication [53].

While most studies of flavour release have focused on the volatile fraction, a few have been dedicated to the in-mouth release of non-volatile compounds. In a primary study, in-mouth conductivity measurements were performed during the eating of cheddar cheese in order to study salt release as a function of texture [54]. The development of an artificial palate with integrated electrodes enabled the continuous monitoring of conductivity in the mouth. The pattern of in-mouth salt release during the mastication process was directly linked to in-mouth cheese breakdown and consequently to its texture. At each chew, a larger quantity of salt was released by firmer and drier cheeses, characterised by a low water content and high salt/moisture ratio. Moreover, the mastication time required to reach maximum salt release was directly related to the softness and creaminess of the cheddars. Springy cheeses were characterized by lower salt release rates.

A similar approach, which also included in-mouth pH monitoring, was adopted to study foods with different textures (peanuts, chips, cheeses and puree) using a dental device equipped with both conductivity and pH sensors [55]. However, the authors highlighted several limitations to this technique. With dry foods, a conductivity signal only appeared when the food was sufficiently hydrated by saliva. With cheeses, other ions contributed markedly to the signal which was not specific to sodium, and as a result the release curves were difficult to interpret. With respect to pH measurements, the buffer effect of saliva was responsible for the poor repeatability of the measurements. And indeed, using such devices, which are somewhat bulky in the mouth, is questionable because they may modify chewing behaviour and stimulate salivation. Smaller systems were therefore developed subsequently in order to overcome these problems. These comprise small electrodes that are placed in the interdental space between two incisors on the lower jaw. They can monitor the salt content in saliva during the chewing of salted gums by means of conductometric measurements and can therefore follow the cyclical and continuous renewal of saliva [44]. Another system has been developed to enable the simultaneous monitoring of changes in conductivity and temperature. The device is fixed on the external surface of an incisor on the lower jaw so that it is not damaged during mastication. Its use has been applied to different foods such as salted peanuts, ham and sausages [56]. One technique consists in sampling saliva from the tongue during chewing using cotton buds and then quantifying sodium ions using specific methods [52]. This was applied to the study of tastants in model cheeses [49]. The quantity and release rates of non-volatile compounds in the mouth were higher when mastication frequency, mastication duration and chewing efficiency increased and when the fat content in the model cheeses decreased. Another similar sampling method consists in the sampling of saliva using a filter paper on the tongue [57]. However, the main drawback of these sampling techniques is the risk of collecting small food pieces along with the saliva. Because the saliva sampling volume is very small under these conditions, the risk of weight errors is very high. The use of saliva spat out into cold tubes and then quickly centrifuged to eliminate all food particles has been preferred in several recent studies. Using model cheeses, it was shown that the release rate and the maximum released salt concentration were higher when the dry matter content and ratio fat/dry matter were lower; however, the fat/dry matter ratio effect was only reported with the higher salt concentration (1.5%) [58].

AROMA RELEASE FROM CHEESE MATRICES

This section focuses on aroma compounds, their interactions with the cheese matrix and their release into the nasal cavity during food consumption.

Aroma Compounds

Physicochemical Properties of Aroma Compounds

Cheese aroma is made up of a large number of aroma compounds from different chemical families with different molecular structures and physicochemical properties. Aroma compounds are small molecules that are volatile at ambient temperature and are capable of reaching the olfactory receptors so that they can be perceived. Their volatility is dependent on both their chemical properties and molecular mass. They are present in very low quantities in foods (less than 1%) and are solubilized in the aqueous and/or lipid phase as a function of their hydrophobicity (logP value). Most aroma compounds are more soluble in oil than in water (logP>1). In order to be perceived, aroma compounds need to be transferred from the lipid phase to the water phase and thence to the vapour phase, so the amount and nature of fat exerts a strong influence on aroma release [59].

Thermodynamic and Kinetic Properties of Aroma Compounds

There are two major factors that control the rate of aroma release from products, namely the volatility of the aroma compounds in the product (thermodynamic factor) and the resistance to mass transfer from product to air (kinetic factor) [60].

Air-matrix partition coefficients between the gas phase and the food matrix at thermodynamic equilibrium provide quantitative information regarding the retention of aroma compounds by the food matrix. They are expressed as the proportion of their concentrations in the air and product phase under equilibrium conditions:

$$K = \frac{C_G}{C_M} \quad (1)$$

where C_G is the concentration of the volatile compound in the headspace and C_M the concentration of the volatile compound in the matrix. A partition coefficient can be expressed using the mass fraction (km), the molar fraction (Ki) or the molar concentration (ki). Therefore, in order to compare values obtained in different units, some conversions are necessary [61].

However, aroma release and perception are time-dependent phenomena, and kinetic parameters supply information that enables a clearer understanding of the behaviour of volatile compounds in food matrices. Diffusion is a spontaneous process by which matter is transported from one part of a system to another by random molecular movements, leading to complete mixing. The molecules in solution move according to rotational and translational movements. Two main factors can impact the diffusion process: (i) obstacles or entrapment effects due to the nature of macromolecules and their structural organization, and (ii) the strength and nature of specific interactions (chemical or non-chemical such as hydrogen bonding) between small solutes (including water molecules and ions) and large food molecules [62].

Modification to Thermodynamic and Kinetic Parameters in a Cheese Matrix

The composition and complexity of food matrices influence the vapour-matrix partition coefficients of aroma compounds as a function of their hydrophobicity and, to a lesser extent, the enthalpy of vaporization [63]. This can be explained by specific interactions between aroma compounds and the non-volatile components present in cheese, such as lipids, proteins and ions, but the nature of these interactions may change because of modifications to the ionic strength, pH, temperature and also the microstructure of the cheese, as presented below.

Influence of Lipids

Cheese products contain large quantities of lipids, food ingredients that exert the most effect on the partitioning of volatile compounds between the product and the vapour phase [64]. A decrease in the air-matrix partition coefficient was observed after increasing the amount of lipid in emulsions, this effect increasing in line with the hydrophobicity of aroma compounds [65]. In model cheeses, an increase in the fat content was shown to induce a decrease in both the air-matrix partition coefficient and the diffusion coefficients for heptan-2-one and ethyl hexanoate, the most hydrophobic compounds [19], whereas no effect, or a reverse effect, was observed for diacetyl which is more soluble in water than in oil (logP = -1.34). The effect of lipid is greater than that of protein; for example, adding just 0.5% miglyol (triglyceride) to water induces a greater decrease in the volatility of nonan-2-one than adding 3% protein (β-lactoglobulin) [66]. In yogurts, an increase in the fat level decreases both the air-matrix partition coefficients [67] and diffusion coefficients [68] for the most hydrophobic compounds.

Interactions between Aroma Compounds and Proteins

Proteins mainly interact with aroma compounds by means of molecular interactions, ionic bonding, hydrogen bonding and hydrophobic bonding [69, 70]. The interactions between β-lactoglobulin and aroma compounds have been widely studied [66, 69-71], because this is one of the principal proteins found in dairy products. The type of bonding depends on both the chemical nature of the aroma compound and the structure of the protein. However, the temperature and ionic conditions of the matrix may also modify the structure of the protein [72]. The strength of these interactions depends on the physicochemical properties of the aroma compound. For instance, the strength of hydrophobic interactions with β-lactoglobulin increases in line with the hydrophobicity (logP value) of the compounds [73, 74], and it has been shown that esters with a long hydrophobic chain are more tightly retained in model systems with protein than short chain esters [75], which induces a decrease in their air-matrix partition coefficients. This retention also induces a decrease in diffusion coefficients [76] and mass transfer coefficients [77], and reduces the perception of odour intensity [78]. Interactions with other proteins (α-lactalbumin, bovine serum albumin, caseins) have also been evidenced [79]. Few data are available on caseins, despite them being present in large quantities in cheeses. Caseins interact with aldehydes by means of covalent and non-covalent bonding [70, 80]. The retention by caseins increases in line with their content [81], but may be inhibited in the presence of water [80]. In dairy products, aroma compounds are more strongly retained by caseins than by whey proteins [82]. In oil-in-water emulsions, sodium caseinate modifies the oil-water interface, inducing a greater resistance to the mass transfer of aroma compounds, as has been observed for ethyl esters [83].

Influence of Salts

The presence of salts (e.g. NaCl) induces an increase in the release of aroma compounds due to a salting out effect [84-86]. Indeed, Na^+ and Cl^- ions are able to mobilise water molecules for their hydration so less water is available for the solubilisation of aroma compounds, which are therefore more released into the vapour phase with higher air-matrix partition coefficients [87]. This salting out effect is more marked with respect to hydrophobic compounds, which are less soluble in water, and occurs not only in water but also in model cheeses [19]. Moreover NaCl modifies the structure of proteins, as has been observed with β-lactoglobulin which is mainly present in its dimeric form in the presence of NaCl because of a modification of electrostatic forces [88]. This will increase the binding of octan-2-one by β-lactoglobulin [89]. NaCl also modifies the structure of the food matrix; for example, a higher NaCl content increases the strength of iota-carrageenan gels and the self-diffusion of ethyl butanoate [90], which can be explained by the greater size of the open space located between the gel chains, resulting in fewer obstacles to the free diffusion of solutes. In model cheeses, the addition of salt may modify the texture by decreasing water activity, increasing firmness and thereby increasing the release of aroma compounds [5].

Influence of Temperature and pH

A rise in temperature increases the air-water partition coefficients according to the Vant'Hoff law, thus enabling the prediction of values at different temperatures. This linear relationship has been used to calculate the energy of vaporization ΔH^0_{eq} of different aroma compounds, which was found to be significantly lower in dairy products (yogurts) [63] or custard [91] than in water. In complex matrices such as dairy products, there is an additional effect of the influence of temperature on macromolecules, and more specifically on proteins [92], which will change the nature of the interactions in play [93].

The influence of pH is more closely related to modifications of protein conformation. For example, between pH 3 and pH 9, the flexibility of β-lactoglobulin was shown to be modified, thus allowing improved accessibility to primary and secondary hydrophobic binding sites and hence an increase in retention, whereas a reduction in retention was observed between pH 9 and pH 11 due to the alkaline denaturation of protein [94].

Influence of Matrix Structure and Texture

The effect of matrix structure and texture on the release properties of aroma compounds has often been studied in model gels [95], although some groups have tried to understand the effect of the microstructure of dairy products on aroma release [96]. In multiphase systems, the composition and nature of proteins and lipids induces different microstructures which will exert different effects on the retention and release properties of aroma compounds. In simple systems such as emulsions, a larger droplet size will increase the release of hydrophilic compounds and decrease that of hydrophobic compounds, because of differences in mass transfer [97]. In yogurts, at the same protein concentration, it was shown that a decrease in viscosity induced by the application of a mechanical treatment resulted in an increase in the intensity of aroma perception [82], and the nature of protein induced differences in microstructure affecting aroma release parameters. In model cheeses, a modification to the protein structure during acidification was shown to induce an increase in viscosity and in the retention of ethyl hexanoate and nonan-2-one [98].

In Vivo Aroma Release during Cheese Consumption

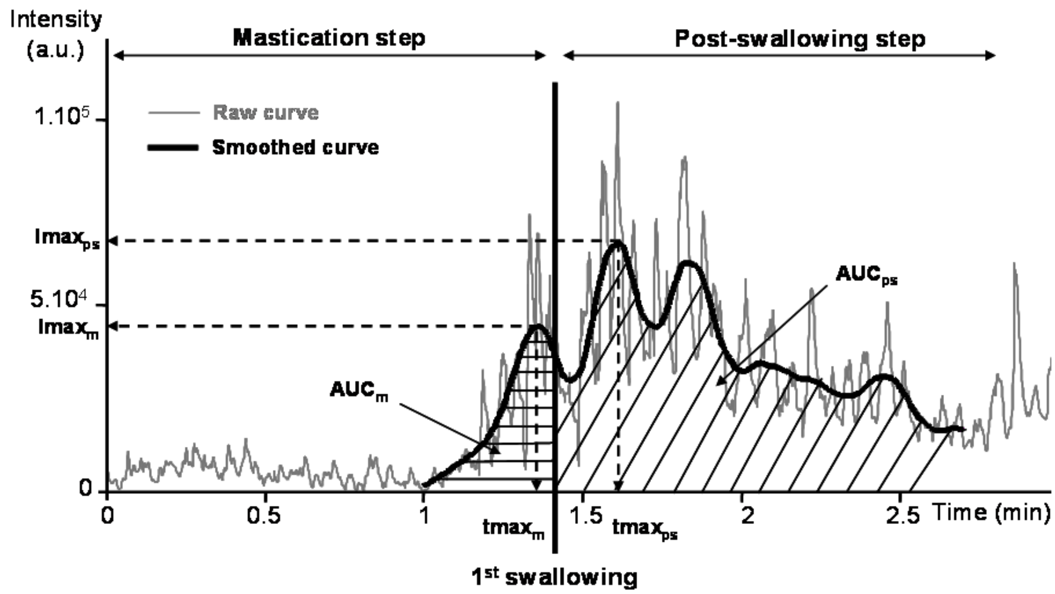

Figure 3. In vivo aroma release followed by atmospheric pressure chemical ionisation mass spectrometry; determination of relevant parameters (AUC: area under the curve, m: mastication step, ps: post swallowing step, Imax: maximum intensity, Tmax: time to reach maximum intensity).

During food consumption, *in vivo* aroma release can be followed using nose-space APCI-MS (atmospheric pressure chemical ionisation mass spectrometry) or PTR-MS (Proton transfer reaction mass spectrometry) [99]. Since their development, these real time *in vivo* techniques have been used extensively to study the impact of the composition and/or texture of a food product on aroma release during chewing. Although the instruments used to study *in vivo* aroma release are the same or similar, there are some differences regarding: i) the parameters extracted from release curves, ii) the averaging of curves obtained in several subjects, and iii) the smoothing of raw curves [96]. The parameters most widely extracted at present are the area under the curve, maximum intensity and the time to reach maximum intensity [100-102], as presented in Figure 3.

It has been shown that aroma release during the consumption of dairy products is influenced by food composition and structure and also by inter-individual variability between subjects [96]. We discuss here the effects of food composition and structure, and then the effects of human physiology, on the release of aroma compounds.

In Vivo Aroma Release as a Function of Cheese Composition and Structure

Cheese manufacturers have to take account of health issues and advisories concerning reductions in fat and salt contents. However, both salt and fat are closely involved in cheese structure, so any reductions will have a considerable influence on not only the texture of the final product but also the release of aroma compounds. Moreover, a reduction in fat content will change the lipid/protein ratio that markedly affects the microstructure of a cheese [103]. Some studies on the effect of proteins on *in vivo* aroma release from dairy products have demonstrated less retention by proteins during the *in vivo* process than during in vitro studies using static headspace measurements at equilibrium, because not only free aldehydes but also some bound aldehydes are released [104]. The type of protein also influences aroma release; the addition of whey proteins decreases the in-mouth release of ketones more than the addition of caseins [105]. The direct effect of lipids has been evidenced using model cheeses [19], resulting in a reduction in aroma release when the lipid content rises, although the dilution effect of saliva needs to be taken into account as it reduces retention in the matrix, as demonstrated in emulsions [65]. An addition of salt to model cheeses was shown not to affect the maximum intensity of *in vivo* aroma release [19], but increased the rate of release [106].

Only a few studies have so far focused on the combined effects of salt, protein and fat on aroma release. In model cheeses, a reduction in the fat content associated with a low salt content induced a decrease in the rate of *in vivo* aroma release [106]. However, model cheeses with a lower fat content presented a higher protein content, thus contributing to a thicker and stronger network with a more rigid microstructure [107]. The effect of salt content differed during the chewing process. An increase in the salt content triggered more rapid aroma release from the protein phase of the model cheese to the oral cavity and thence to the nasal cavity, inducing a higher rate of aroma release. Model cheeses with a higher salt content presented a larger droplet size which reduced the transfer of hydrophobic aroma compounds from the fat to the aqueous phases; the release of nonan-2-one, a more hydrophobic compound than ethyl butanoate therefore occurred later after swallowing the cheese with a higher salt content (Figure 4). This means that the direct effect of cheese composition on *in vivo* aroma release is difficult to dissociate from the effect of cheese microstructure and texture.

In low-viscosity dairy products such as yogurts, an increase in viscosity induces a decrease in the air-matrix partition coefficient, the diffusion coefficient and the amount of aroma release during consumption [82, 108], with a longer time required to reach maximum intensity and a lower level of perceived aroma intensity [82]. With more viscous products [109] or hard cheeses that required mastication [98, 110], the rate and total amount of release were higher for the firmest products. This could be explained by an adaptation of mastication behaviour to hardness, leading to the formation of numerous particles increasing the total surface area and thus mass transfer from the product to the saliva and air.

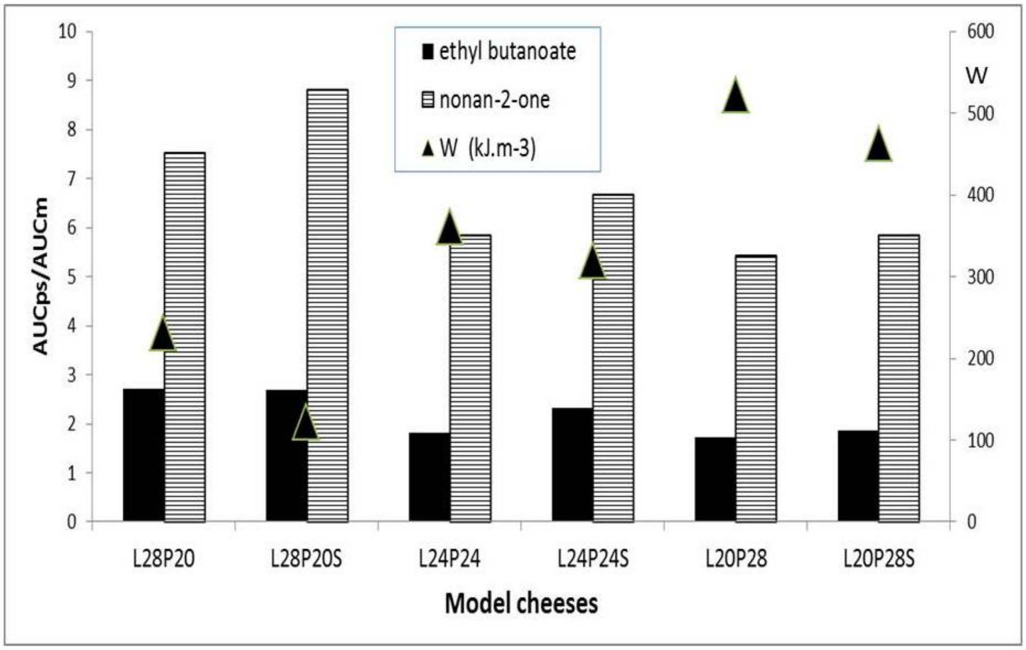

Figure 4. In vivo release of ethyl butanoate and nonan-2-one, ratio between the areas under the curve after swallowing (AUCps) and during mastication (AUCm), as a function of cheese firmness determined by work to maximum deformation (W). Model cheeses vary in lipid (L)/protein (P) ratios and salt content (s means addition of salt).

In Vivo Aroma Release as a Function of Oral Physiology

In addition to the effects of product composition and structure on *in vivo* aroma release, considerable inter-individual variability exists between the subjects who consume the products, in terms of the rate and total amount of aroma released [96]. These differences can partly be explained by differences in food oral processing, such as mastication, progressive insalivation, formation of a bolus by lubrication, and the agglomeration of food particles, swallowing [111] or variations in oral volume [112]. Moreover the consumption protocol may modify aroma release curves [113].

The Composition and Flow Rate of Saliva Affect In Vivo Aroma Release

Saliva can affect aroma release and perception by diluting flavour compounds [114, 115], because of interactions between aroma compounds and saliva constituents [116], by enzymatic activity or by its buffering capacity [117]. However, these effects depend on the aroma compound considered. For example, in dairy products such as a cream-style dressing, dilution with artificial saliva decreases the release of hydrophilic compounds more rapidly than that of hydrophobic compounds [114], because of a different partitioning between the oil and water phases. Of the salivary proteins, mucins are present in the largest quantities; their retention effect on aroma compounds cannot just be explained by their hydrophobic effect [116] and they may be modified by an addition of salivary salts which changes their conformation state. At the levels found in the mouth, salivary α-amylase is capable of hydrolysing bonds within amylose and amylopectin and thus lowering starch viscosity within seconds, inducing a reduction in aroma release [118]. In dairy products, the action of lipase may induce the formation of aroma compounds from lipid hydrolysis [119]. Salivary esterases are endowed with a catalytic activity which is similar to that of lipase but they act on shorter compounds such as short-chain fatty acids or esters. It has been suggested that they are involved in ester hydrolysis and are responsible for flavour alteration [120].

Other salivary parameters can also influence *in vivo* aroma release. Theoretical models have predicted that a change to the salivary flow rate can induce a variation in aroma release [121]. However, different studies conducted in human subjects did not determine any direct correlations between salivary flow rates and *in vivo* aroma release, either using model cheeses [111] or following the consumption of a mint pastille [122]. More recently, in a study on model cheese, the influence of the amount of saliva incorporated into the bolus was shown to reduce the rate of release of the most hydrophilic compounds [123]; this was also confirmed using a release model fitted to experimental data [124]. However, the amount of saliva incorporated into the bolus could differ markedly depending on the composition of the cheese, and indeed, more saliva was produced and thus incorporated during the consumption of low-fat and formed cheeses because of longer chewing duration. The smaller quantities of ethyl propanoate released could be explained by a higher dilution of this more hydrophilic compound in the saliva, whereas few effects were observed regarding nonan-2-one, which is a more hydrophobic compound during mastication [123].

Mastication Behaviour Affects In Vivo Aroma Release

Mastication plays a key role in the process of aroma release from cheese products. It involves the gas phase transfer of volatiles from the mouth to the pharynx where they are swept through the upper airways to the nose by expired air from the lungs. The mastication process is known to adjust to the different textural properties of foods. In other words, the harder the foods, the more chewing cycles are required to reach the swallowing threshold [125]. In subjects who adapted their chewing behaviour to different product characteristics, the results concerning the rheological properties of the bolus tended to show that hard and low-fat cheeses, which required high total muscle work to be eaten, produced boluses that were harder and broke down less than soft and high-fat cheeses [126]. An increase in masticatory parameters due to greater firmness has also been shown to increase the amount of aroma released in the nasal cavity [110, 123]. However, this effect is dependent on the properties of the aroma compounds involved. More hydrophilic compounds are more likely to be influenced by the firmness of the cheese and are released more from firm cheeses during the mastication step, whereas more hydrophobic compounds such as nonan-2-one tend to be retained more in fat during the mastication step and released more after swallowing. Thus an increase in cheese firmness has less effect on aroma compound release than a rise in fat content which reduces both the rate and total quantity of compounds released [123].

However, it has been observed that an increase in masticatory behaviour also increases the salivary flow rate [44, 127], which means that aroma release cannot be explained by just one type of oral parameter.

Swallowing is a Key Step in In Vivo Aroma Release

When consuming liquid foods, the mouth in most subjects can be regarded as a closed system for as long as no swallowing occurs or the base of the tongue is not lowered deliberately or unconsciously due to distinct mouth and tongue movements [128]. Opening of the velum occurs mainly at swallowing, allowing the transfer of aroma from the oral cavity to the nasal cavity. However, oral movements have been shown to contribute to the total quantity of aroma released, although swallowing events are the principal contributors, followed by tongue movements, jaw movements and the first swallowing event [122]. The relative importance of each event may vary depending on the foodstuff being consumed and the regularity of each process [129]. The initiation of swallowing, which is voluntary, has been thought to depend on separate thresholds for food particle size and particle lubrication, but at the swallowing threshold, bolus cohesiveness seems more important that particle size reduction [126, 130]. After swallowing, a residual film of saliva (or a mixture of saliva and food) remains on the pharyngeal mucosa and participates in aroma release after swallowing [57]. It has been suggested that aroma release from liquids after swallowing results from this residual film [131]. However, inter-individual variations in oral physiology will induce different modes of release. When consuming model cheeses, aroma compounds were released in some subjects between the start of the chewing phase until the end of consumption, whereas they were only released after swallowing in others [96]. In the case of liquid dairy products, three groups of subjects were observed as a function of their release curves [72], but the maximum intensity of aroma release was always achieved after swallowing and the total amount of aroma released was greater during the post-swallowing step.

FLAVOUR PERCEPTION

Effect of Food Matrix Composition on Salty Perception

As a general rule, fat content affects salty perception. An increase in fat content causes an increase in saltiness intensity in a single emulsion [132], jellied dairy products [133], cheese products [134] and model cheeses [49, 58]. However, proteins exert an opposite effect on saltiness, the intensity of which decreases when the protein content in foods is increased. This effect has been attributed to the binding of sodium ions with the proteins which are then no longer available to activate taste receptors. In this way, the binding of sodium ions with caseins has enabled the addition of less salt to tomato soup [135]. A similar observation was also made regarding gluten [136]. On the other hand, the presence of lactose in milk is responsible for a sweet taste that can partially mask saltiness [135].

Saltiness perception can be explained by in-mouth salt release when eating potato chips [137] or salted gums [44]. With other foods such as model cheeses [49, 58], temporal saltiness perception was not influenced by the same parameters as salt release, suggesting perceptive interactions between saltiness and other perceptive modalities.

Effect of Texture on Salty Perception

In solutions containing a higher concentration of biopolymers, the intensity of taste and aroma perception was seen to be lower because of greater viscosity [138]. This was confirmed with dairy products, where saltiness intensity was found to be weaker with more gelled and less liquid products [139]. As for firmer products such as bread, density can also affect saltiness perception. For example, a denser bread was perceived to be less salty [133], while density did not affect in-mouth salt release. In terms of the dynamics of perception, the predominance of temporal perception measurements (TDS) has shown that saltiness perception tends to be perceived at the end of bread consumption. The contact area between the food bolus and saliva increases during the eating process, allowing the stimulation of more taste receptors and consequently inducing an increase in saltiness intensity [132, 140]. Some authors have suggested that fat coating the surface of the mucous membrane on the tongue may reduce contact between taste receptors and salt [49, 141]. However, sodium ions will be able to pass through the fat film on the tongue and reach the taste receptors, mainly because of their small size and despite interactions between fat and the mucous membrane [142, 143].

Intermodal Perceptive Interactions between the Perception of Aroma and Saltiness

As well as physicochemical interactions, many studies have reported cross-modal perceptive interactions between taste and aroma [144, 145]. These taste-aroma interactions are dependent on the aroma/taste pair [146]. For example, garlic aroma [147], and sardine, bacon, anchovy, peanut, tuna and Roquefort aromas [148] enhance salty perception. The concomitance of retronasal olfaction and taste perception allows such cross-modal perceptive interactions [148-151]. These interactions have mainly been studied in water solutions and were dependent on the salt concentration. A phenomenon of saltiness enhancement by congruent aromas was observed at low and medium salt concentrations (0.01 or 0.02 M NaCl), but the effect was no longer observed at a higher salt concentration (0.04 M NaCl) [151]. Similar results have also been observed with model cheeses [152]. In particular, it was seen that the enhancement of saltiness by aroma was modulated by texture, and that this effect was not observed with a harder texture. In ternary odour-sour-salty solutions, sourness enhanced saltiness additively with salt-related odours. This combination was found to compensate for a reduction of more than 20% in the salt content [153].

Intramodal Perceptive Interactions between Tastes

In cheeses, the water-soluble extract plays a fundamental role in overall flavour [154]. It notably contains many non-volatile compounds with active taste properties, such as mineral salts, organic acids, amino acids, lactose and peptides, which are responsible for the saltiness, sourness and bitterness of this extract. These taste attributes have been shown to be responsible for intramodal perceptive interactions when the different stimuli are contained in mixtures [155]. For example, in goat cheese, bitterness was found to be due to the bitter taste of calcium and magnesium chlorides, which is in turn was partially masked by the saltiness of sodium chloride [156, 157]. Moreover, the additive effects of salts on saltiness have been reported, enhancing the effects of sodium chloride on sourness because of the balance between phosphate and lactate species with respect to the pH value. In Camembert cheese, the effects were found to be different. The sourness of a Camembert water-soluble extract could be explained by the slightly sour note due to H_3O^+ ions in the solution, strongly enhanced by the saltiness of sodium chloride [158].

Conclusion

Cheeses are complex processed foods whose organoleptic quality results from a particular association of taste, aroma, texture and structural properties, each of which endow each cheese with its overall specific character. Two important ingredients that are closely involved in these properties are fat and salt, which cannot be dissociated from cheese. However, if consumed excessively, these ingredients can be responsible for conditions such as hypertension, cardiovascular disease and obesity. Their multifunctional role in cheeses has qualitative and quantitative implications for their composition. Consequently, detailed knowledge of these properties and their interactions, of the dynamic mechanisms that lead to in-mouth flavour release and perception, and of their microstructure, should enable the reformulation of cheeses so that they can comply with health guidelines. This needs to be done by fine-tuning this reformulation through the engineering of the technological parameters that are specific to each product, in order to preserve the typical qualities of each cheese and to ensure that they remain acceptable to consumers, thus preventing any negative impact on the economics of the food industry.

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