Peer-reviewed | Manuscript received: June 29, 2015 | Revision accepted: November 23, 2015

Odor and Nutrition

Part 2 – Traits of Odors

Matthias Kotthoff, Schmallenberg; Svenja Nörenberg, Vaterstetten

Small cause, great odor difference:
The isomer (–)-carvone smells strongly of mint, whereas (+)-carvone is an important key food odorant of caraway.

In the first part of the special "odor and nutrition" the anatomical and physiological basis of smell, as well as the fundamental vocabulary of aroma and olfactory receptor research have been outlined. This second part targets the question, which odorants exactly make up the characteristic smell of food.

Summary

Odorants have a major importance for the evaluation of food. Thousands of odorants occur in foodstuffs, but only a small minority of them plays a role for the conscious perception of food aromas. Some odorants can be quite similar on the basis of their chemical properties but strikingly different in their sensory properties, yet others surprise with sensory similarity despite fundamental structural differences. Food aromas are inimitably composed of three up to 40 individual odorants, so that the composition of the final odors is subject to a complex combinatorial code. This makes it challenging to copy food odors in easy ways. This degree of complexity is further increased by inter-individual differences in the perception, which likely also adds to the generation of individual food preferences.

Keywords: smell, odorants, odor research, odor, sensory science, pharmacology

Citation:
Kotthoff M, Nörenberg S (2016) Odor and nutrition. Part 2: traits of odors. Ernahrungs Umschau 63(1): 22–30

This article is available online:
DOI: 10.4455/eu.2016.005

Introduction

Foods are complex composed matrices of macronutrients, versatile micronutrients such as vitamins or antioxidants, and moreover contain water, many minerals, and/or gases. All these molecules can either be odorants themselves or can be transformed into odorants in direct or indirect ways. Many interactions between food components, e.g. catalysis by metal ions or on surfaces, radical and redox reactions may influence the release, formation and transition of odorants. Also external influences like photolysis, oxidation due to atmospheric oxygen, or condensation reactions during drying may occur. In food, as a biological system, also enzymatic reactions occur, especially after the disruption of cellular integrity by chopping, grinding or mixing. Further complex reactions may happen when the food is finally processed, most importantly when food formulations (i.e. recipes) are being processed: heating, cooling, freezing, drying, mechanical stress, hydrolyses in different pH-milieus, extrusion, sheering forces, frying, treatment with smoke, extended storage, fermentations, and many more processes.
It is expected, that in food about 8,000 volatile components may occur, of which – however – only a small fraction is of importance for the respective perceived food aroma [1].

Odorants playing a role in a respective food aroma are referred to as key food odorants (KFO).

Many of these compounds arise from the same chemical reaction pathways, and thus have similar structures or belong to the same chemical classes. Hence, similar structures not necessarily have similar sensory qualities nor sensory thresholds: pyrazines for example emerge from the non-enzymatic browning reaction (Maillard-reaction) and play a major role for the aroma profile of several foodstuffs. Up to 70 alkyl pyrazines (compare e.g. 1 to 3 in ◆ Figure 1) have been described in food [2]. Of these, however, only few contribute to the perceivable food aroma, only these few have odor thresholds low enough to be below their concentration in a respective food.

This quotient of the odorant concentration in food and its odor threshold is an important measure to allow for

$$\text{OAV} = \frac{\text{c (Odorant)}}{\text{Odor Threshold}}$$

an estimation of the odorant's importance in the food. This quotient is referred to as the Odorant Activity Value (OAV) [3].
One principal requirement for an odorant to actively contribute to the total aroma of a given food is that its OAV is > 1. This indicates that its concentration exceeds the odor threshold. The OAV is a major, but not exclusive, initial parameter to estimate whether an odorant can be considered a KFO.

For a final elucidation of food odorants, usually **reconstitution and omission experiments** are performed. As part of these, the food odorants are being recombined according to analytical results in a comparable matrix and evaluated by a sensory panel (compare p. 26 chapter "odorants and their mixtures"). If the properly prepared odorant recombinant superimposes optimally with the native food aroma, it is being started to omit individual odorants. If the aroma of the recombinant changes significantly, the omitted odorant is obviously important for the food aroma and must be considered a KFO.

Since in real food several odorants always appear in parallel, virtually no food exists, whose full aroma profile is defined by only one single odorant.

The situation complicates in the case of volatiles and odorants that have no intrinsic smell or that smell only very weak. Due to pharmacological effects (Ernährungs Umschau 5/2015: Odor and nutrition. Part 1: Fundamentals of smelling) they may, however, contribute to the food aroma by means of a *modulatory* impact (i.e. pharmacology).

Similar chemical structures, different sensory impact

The olfactory disparity of chemically similar volatiles is reflected on a qualitative as well as on a quantitative level.

Differences in odor thresholds

The already mentioned pyrazines reflect an important group of heterocyclic odorants which impact the aroma of many versatile foods, e.g. roasted or fermented ones. Among these foods are cocoa, coffee or bakery products, but also roasted meat. Mainly differentially alkylated pyrazines occur, all smelling vaguely earthy, moldy, roasty, or caramel like, but may vary harshly in their odor thresholds. Important and very potent odorants are e.g. 2-ethyl-3,5-dimethyl pyrazine (1 in ◆ Figure 1) and 2,3-diethyl-5-methylpyrazine (2 in ◆ Figure 1) with odor thresholds of less than 10 ng/L in water. The 2,3,5,6-tetramethylpyrazine (3 in ◆ Figure 1) occurs quite often and in comparably high concentrations, however, due to its high odor threshold of above 1 mg/L in water it is almost odorless and of no relevance to food aromas at all [2].
Similar observations were made with the so called wine-lactone (3a,4,5,7a-tatrahydro-3-6-dimethyl-benzofuran-2[3]-one) (4 in ◆ Figure 1) which plays an important role not only in wine. The wine lactone may

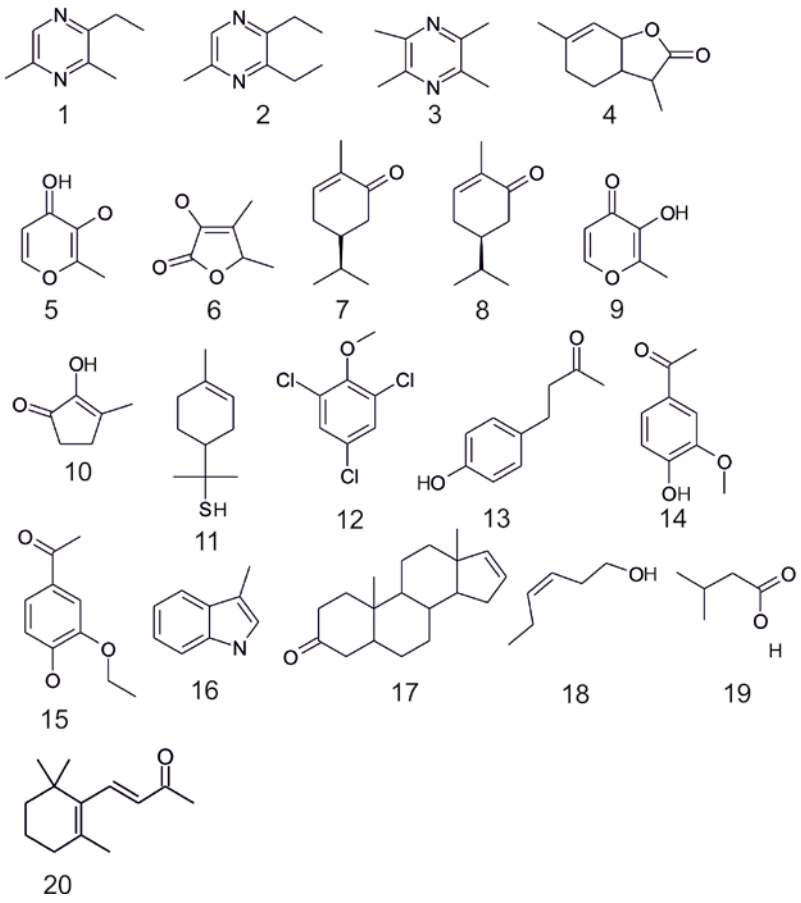

Fig. 1: **Chemical structures of exemplary odorants**
(explanations and names of substances can be found throughout the text)
1 = 2-ethyl-3,5-dimethylpyrazine; 2 = 2,3-diethyl-5-methylpyrazine; 3 = 2,3,5,6-tetramethylpyrazine; 4 = 3a,4,5,7a-tetrahydro-3,6-dimethyl benzofuran-2[3]-one; 5 = 2,5-dimethyl-4-hydroxy-3(2H)-furanone; 6 = 3-hydroxy-4,5-dimethyl furan-2(5H)-one; 7 = (–)-carvone; 8 = (+)-carvone; 9 = 3-hydroxy-2-methylpyran-4-one; 10 = 2-hydroxy-3-methyl cyclopent-2-en-1-one;11 = 1-p-menthene-8-thiol; 12 = 2,4,6-trichloroanisol; 13 = 4-(4-hydroxyphenyl)-butan-2-one; 14 = vanillin; 15 = ethylvanillin; 16 = skatole; 17 = androstenone; 18 = cis-3-hexen-1-ol; 19 = 3-methyl butyric acid; 20 = ß-ionone

occur in eight different enantiomeric[1] forms, whose odor thresholds spread over eight magnitudes. In the case of the eight possible wine lactones, only the (3-S,3aS,7aR)-enantiomer with an odor threshold of around 100 pg/L air plays a role, e. g. in wine, whereas the (3R-3aR,7aS)- and the (3R-3aS,7aS)-enantiomers are altogether odorless [4].

Differences in odor qualities

Striking differences of chemically quite similar odorants arise also on a qualitative level. The 2,5-dimethyl-4-hydroxy-3(2H)-furanone (5 in ◆ Figure 1), also known under its trade name Furaneol®, e. g. smells sweet, like caramel, and appetizingly like strawberry, in which it also adds to the total aroma profile as a KFO [5, 6]. However, the structurally similar sotolon (3-hydroxy-4,5-dimethyl-furane-2[5H]-one) (6 in ◆ Figure 1) smells intensely herbal and resembles lovage, whose aroma it shapes indeed [7].

A very important group of odorants are represented by **terpenes** which originate from the mevalonate pathway. Despite the fact that their structural versatility is quite restricted (aroma relevant terpenes consist of 10, 15 or 20 C-atoms and rarely harbor any hetero atoms), the terpenes express an impressive width of odor impressions and shape the aroma of many plants, herbs, and spices. A very interesting and popular terpene is carvone, which harbors one optical center and thus occurs in two enantiomeric forms [(+/–)-carvone]. While the (–)-carvone (7 in ◆ Figure 1) strongly smells of mint and outlines the basic smell of mint, the (+)-carvone (8 in ◆ Figure 1) smells intensely of caraway and shapes its respective aroma profile. Despite both molecules exhibit strikingly different odor qualities, their odor thresholds are quite comparable [8].

Different chemical structures, similar sensory impact

Interestingly, there are also odorants which differ structurally, but nevertheless exhibit comparable sensory characteristics. The already mentioned 2,5-dimethyl-4-hydroxy-3(2H)-furanone (5 in ◆ Figure 1), 3-hydroxy-2-methyl-pyran-4-one (9 in ◆ Figure 1) as well as 2-hydroxy-3-methylcyclopent-2-ene-1-one (10 in ◆ Figure 1) e. g., smell pleasantly roasty and caramel-like. They all originate from the non-enzymatic browning reaction (Maillard-reaction) and thus frequently occur all at once. Possibly, it therefore is not evolutionarily advantageous to have the ability to distinguish the three odorants of the same origin with specific odorant receptor repertoires.

However, there are certain groups of chemical classes that can be assigned to some typical qualitative odor impressions if the functional group mainly rules the molecule's characteristics: Most **esters** smell fresh and fruity and are, indeed, major components of the aroma

[1] Enantiomeres are molecule variants (mirror-image isomers) of equal chemical formula yet different spatial structure.

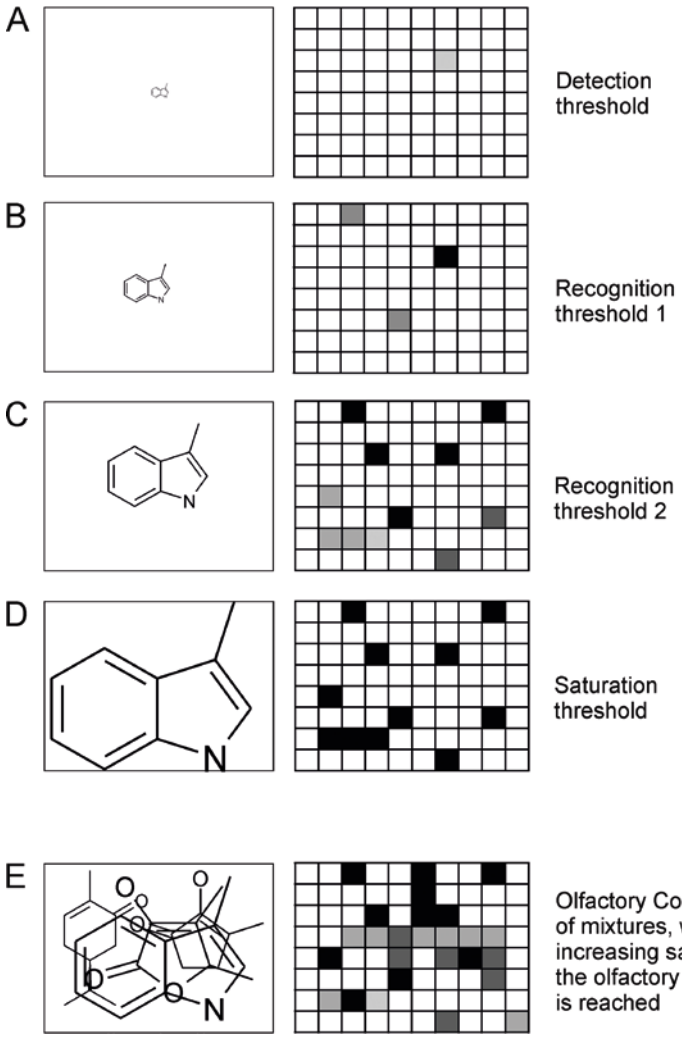

Fig. 2: **Visualization of the physiological basics of sensory thresholds**
The depicted activation patterns only serve as a tool for visualization and are not the result of experimental research.
A: Detection threshold: Only the most sensitive odorant receptor is activated.
B and C: Recognition thresholds: Specific activation patterns reflect the typical recognition profile of odorants or complex aromas.
D: Saturation threshold: All specific odorant receptors are saturated with odorant molecules, an increase of odorant concentration does not trigger a more intense odor sensation.
E: Activation pattern of odorant mixtures: The more odorants make up a mixture, the more complex the resulting activation pattern will be, and the lesser the impact of individual odorants on the total aroma.

profile of fresh fruits and juices; **pyrazines** (see above) smell completely different. **Thiols**, or **sulfur containing volatiles** in general, smell in higher concentrations, very often unpleasant, despite the fact that many sulfur containing odorants are very important components of natural and synthetic aroma profiles and formulations.

Predictability of aroma quality and quantity

Concluding the aforementioned, it is not possible to predict the sensory characteristics of volatiles only by means of their chemical structure. Concerning this, the coding of the sensory impression, resulting from the combinatorial code of receptor activation, is way too complex and still understood insufficiently.

Promising starting molecules for the initiation of structure function prediction models of odorants are linear molecules with only one functional group. For those it is possible, by means of chemical synthesis, to generate so called homologous series of a substance in which either the molecule length varies, or the position of the functional group within the molecule moves. Subsequently, the sensory characteristics of the synthesized molecules are determined and compared to one another. This was performed, e. g., with alkylated thiols [9]. It was shown that from all researched classes, the molecules with six to seven carbon atoms were those with the lowest odor thresholds, with the variations rarely affecting the odor quality. Similar work was performed on unsaturated ketones. The odor threshold minima observed in this study were in the range of six to eight/nine carbon atoms chain length. Notably in the case of linear unsaturated ketones, also the odor quality depends on the chain length as well as on the position of the enol and keto groups within the respective molecules. The qualities range from pungent (C5) to metallic and vegetable-like (C6 to C7), to mushroom-like (C8) and even to citrus-like and soapy (> C8) [10].

By applying such research, the physical-chemical data of the molecules (i.e. homologues series) can be correlated with their sensory characteristics and be transformed into so called QSAR models (Quantitative Structure Activity Relationships). On the basis of such models, Polster and Schieberle were able to predict the odor thresholds of alkyl thiols by means of the spatial structure in the limited horizon of the homologous series [11].

Perception of odorants

Partly very low effective concentrations

Food odorants can be very potent. A very impressive example is the sulfur containing 1-p-menthen-8-thiol (11 in ◆ Figure 10) which is a key food odorant in grapefruit and has an odor threshold as low as 0.02 ng/L water. 1-p-menthen-8-thiol is the most potent odorant known. By way of illustration: the weight of as few as 6 sweetener pills of this substance would suffice to aromatize Lake Constance to be grapefruit-like perceivable for human.

The sulfur containing odorants belong per se to the most sensitively perceived volatiles. Why so is controversially discussed up to now. The sulfur atom is readily polarizable and thus easy to coordinate inside possible binding pockets of odorant receptors. There is some research targeting the role of metal ions (especially zinc) for the perception of thiol molecules [12, 13]. Moreover, it is remarkable that unpleasant odorants often have notable low odor thresholds. A good example is 2,4,6-trichloroanisol (12 in ◆ Figure 1) which, e. g., causes the corky note of wine. 2,4,6-trichloroanisol is generated by microorganisms from chlorinated compounds[2] used during cork production and wine fermentation. It has an odor threshold of 0.01 µg/L in water and can be detected by humans even in traces [14].

Neuronal odor processing

Any single odorant alone produces a specific, concentration dependent two dimensional pattern of activated neurons. Any mixture of different odorants produces another very specific concentration dependent, distinctive odorant fingerprint of activated neurons. This activation pattern is encoded from quality and quantity of activation as a sum of all individual activation patterns of the respective odorants in the mixture and the resulting pharmacological modulations. Recently, Bushdid et al. extrapolated the total number of qualitatively distinguishable aroma impressions to about 1 trillion [15].

„By way of illustration: the weight of as few as 6 sweetener pills of this substance would suffice to aromatize Lake Constance to be grapefruit-like perceivable for human.“

Odorants and their mixtures

Since in the real world we are always exposed to mixtures of different chemical compounds (i.e odorant mixtures) and never to purified specific molecules, the knowledge of the sensory properties of individual volatiles is only of limited value. Naturally occurring food aromas consist only in very simple cases of only a few odorants. Taking butter as a simple example, its aroma-profile is constituted of only three substances: butyric acid (sweaty), 2,3-butandione (buttery), and δ-decalactone (coconut-like) [16, 17]. In more complex cases the full aroma-profile may be constituted of far more than 20 volatiles, e.g. the aroma profile of coffee (27 key food odorants), or cognac (36 key food odorants) [1].

However, there are many foodstuffs whose aroma profiles are qualitatively dominated (but not fully represented) by single odorants. Such important substances are referred to as character impact compound for a respective food. Examples are mint ([–]-carvone), caraway ([+]-carvone), raspberry (4-[4-hydroxyphenyl]-butan-2-one, also known as raspberry ketone; 13 in ◆ Figure 1), or vanilla (4-hydroxy-3-methoxybenzaldehyde, also called vanillin; 14 in ◆ Figure 1).

The character impact compound is sufficient to assign an aroma to the respective food, yet the character impact compound alone does not represent the full aroma profile. For this, the remaining components of the full aroma profile are probably missing to complete the complex recognition pattern of odorant receptor (OR) activation (compare part one of this article series).

In the production of convenient or low-price products, e.g. certain sweets, the representation of the authentic full aroma profile is waived for the sake of economic favor, but with curtailment of sensory appearance.

Combinatorics: the key for understanding sensory phenomena

There are strong hints that each of the more than 400 odorant receptor types can be activated by a more or less wide spectrum of odorants, and that in turn, some odorants can activate several receptor types [20]. Sometimes the odorant receptor

[2] The corky note of wine not only arises from the actual cork but also from chlorinated bleaching and disinfecting agents. Therefore it can also occur in wines with a screw plug.

The natural aroma of original Bourbon-vanilla is a quite complex composition of odorants and is only in part represented by the character impact compound vanillin. Vanillin does not generate the full and identical neuronal activation pattern as Bourbon-vanilla with its secondary components and 'minor' odorants. Vanillin can be produced with biotechnological methods from eugenol or lignin (the molecular scaffold of wood) in a convenient way [18]. In many cases the very similar synthetic odorant ethyl vanillin (15 in ◆ Figure 1) is used, which has a three- to four-fold lower odor threshold and can thus be applied in lower concentrations [19]. The aroma of native vanilla can hardly be copied or imitated in an economic manner, so that for high-quality products only real bourbon-vanilla may be used.


© Dubbotina Anna/Fotolia

The controversially discussed issue whether biotechnologically produced vanillin may be considered a natural odorant shall not be part of this article.

The knowledge on the molecular interrelationships in odor perception bears also a very high economic potential.

types are denoted generalists (wide odorant spectrum) [21] or specialists (tough odorant spectrum) [22]. This gives rise to the existence of an olfactory code, specific for any olfactory impression.

Olfactory white

Similar to vision, also in olfaction there is a condition where all impressions overlap. What is known as "white" in vision, and results in the simultaneous activation of all color sensors (cones), has been described as "olfactory white" in olfaction. In this condition many receptor types are activated simultaneously in an overlapping fashion, thus, no specific olfactory code (activation pattern) can be inferred anymore (compare E in ◆ Figure 2). According to Weiss et al. mixtures of more than 30 different odorants are required to generate this impression [23].

Molecular definition of sensory thresholds

Important parameters for sensory science can also be drawn from the combinatorics on the odorant receptor level: **detection threshold, recognition threshold and saturation threshold.**

In the area of the **detection threshold**, the odorant concentration is just high enough to activate the most sensitive odorant receptor in a way that the presence of a "smell" is barely perceivable (compare A in ◆ Figure 2). At the detection threshold, it can only be decided whether there is something that smells or that does not smell, but the impression cannot be assigned qualitatively. Most likely, this threshold is defined by the odorant receptor with the highest sensitivity (the lowest EC_{50}, part one of this article) for the respective odorant.

With increasing odorant concentration, more and more odorant receptors are most likely activated and thus, the specific activation pattern (which reflects the specific olfactory code) is established and the concentration reaches a level where its quality can be recognized. The concentration, from which the stimulus can be assigned to a specific sensory quality, is referred to as the recognition threshold (compare B in ◆ Figure 2).

It is possible that a single odorant can be assigned different odor qualities in a concentration dependent manner. 3-methylindol (skatole, 16 in ◆ Figure 1), e. g., one of the most potent odorants in feces, has a flowery smell in small concentrations and is an important ingredient of cosmetic aroma formulations and perfumes to which it contributes with a full and harmonic aroma body. Consistent with this model, skatole only activates all odorant receptors that make up the feces-like, urinous smell only at higher concentrations (compare C in ◆ Figure 2).

For the molecular definition of the **saturation threshold** (compare D in ◆ Figure 2) at a certain odorant concentration, all odorant specific odorant receptors would be saturated, and a further increase of odorant concentration would not anymore allow for a qualitative differentiation.

Reasons for off-flavors

Odorants can contribute to the characteristic food odor, but can also cause off-flavor [8]. 2,3-butandione e. g. is an important contributor to the aroma of butter (see above) and is also

present in beer. However, if the concentration of 2,3-butandione exceeds the level of 0.13 mg/L beer, it is recognized as unpleasant. If the concentration is further increased to > 0.35 mg/L, it may cause an off-flavor in beer [8].

Further reasons for the appearance of off-flavors can be the absence of food specific key food odorants or the occurrence of dissimilar odors of foreign sources. The generation of malodors causing off-flavors is often the result of chemical or microbiological reactions (e.g. oxidation, non-enzymatic browning, and interaction of food constituents, light- or enzyme induced reactions) or contaminations [24]. Especially chlorophenols and chloroanisoles, such as the above mentioned 2,4,6-trichloroanisole, are well known chemicals that may migrate via air, water, or packaging materials into foodstuffs and can be perceived even in traces due to their very low odor thresholds. A fruity off-flavor for instance was observed in carbonized mineral waters which could be drawn back to the migration of acetaldehyde from polyethylene terephthalate (PET)-containing bottles [25, 26].

The identification of off-flavor causing odorants is essential for the development of targeted avoidance strategies. In odor research, specific sensory and analytical strategies are applied. In gas chromatography olfactometry coupling, volatile substances from food are separated by chromatographic methods and are detected by sensory trained personnel by nose. With this elaborate technique the odor qualities as well as the relative intensities of individual odorants can be determined. By means of the high performance of the human nose, this analytical technique is especially suited for the detection of very potent malodors occurring at concentrations below the resolution and detection power of modern analytical devices. Applying this method allowed identifying a medicinal off-flavor in mineral waters caused by 2-iodphenol and 2-iod-4-methyl phenol [27].

How many key food odorants are there in foodstuffs?

In a large scaled meta-analysis performed by Dunkel et al. all available publications on key food odorants were assembled and evaluated [1]. This study provides a comprehensive overview over the current state-of-the-art related to key food odorant research. In more than 220 researched foodstuffs covering all product groups, a total of 226 individual odorants could be identified to be key food odorants. Despite the occurrence of more than 8,000 total volatiles in foods only a small minority of less than 2 % of all volatiles encodes for the full aroma of virtually all available foodstuffs. Of these 226 key food odorants 16 individual compounds occur in more than 25 % of all foodstuffs. Due to their widespread prevalence, these important key food odorants are characterized as generalists. They mainly originate from common precursor substances such as carbohydrates, amino acids or fatty acids. Besides these generalists there are many specific odorants that only occur in some small food groups, particular foods or ingredients such as herbs and spices. They are denoted as specialists and originate from precursors that only occur in specialized metabolic pathways of some certain raw commodities. In total there were 151 key food odorants identified that occurred in less than 5 % of all analyzed foods.

By their mode of formation odorants can be differentiated into primary and secondary odorants. Odorants already present in the raw commodity are referred to as primary odorants. Secondary odorants however only form during processing steps such as heating, oxidation, enzymatic treatment, and so on, from (mostly non-volatile) precursor substances. The typical smell of a cucumber for example is only generated and released after the fruit is cut. The well-known smell of garlic is formatted upon cleavage of alliin into pyruvate, ammonia, and the character impact compound of garlic allicin [28]. The Maillaird-reaction is an important reaction in formation of volatiles (see above) by thermic exposure of foodstuffs [8].

The relevance of the sense of smell for individual food choice

The individual perception of smell influences our food choice and thus impacts our nutrition. This is quite obvious in the case of complete or unspecific anosmias, where the smell of odorants cannot be perceived at all or only to a limited extend (part 1 in Ernährungs Umschau 5/2015). Both are rather pathologic scenarios, which the concerned persons are well aware of, and that require an active handling. Yet which impact physiologically "normal" individual differences – mediated by single nucleotide polymorphisms (SNPs) in the genes for odorant receptors – have on the individual daily diet is largely unknown. In the past, some *in-vitro*-experiments could identify several SNPs to be associated with specific anosmias. A prominent example is androstenone (17 in ◆ Figure 1), a pungent, ruinous, and sweaty smelling odorant originating from the steroid metabolism of male pigs. In non-caponized boars androstenone (together with skatole and further odorants) enriches in the fatty tissue of the animals and may disqualify the meat from consumption due to malodor. But not every human individ-

ual is capable of smelling androstenone; about every other harbors a mutation in the corresponding gene OR7D4, and renders the expression product unable to be activated with androstenone [29]. In turn, only customers abler to smell the ruinous-sweaty note of androstenone are likely to deny the consumption of meat polluted by androstenone.

There are further examples, e.g. *cis*-3-hexen-1-ol (18 in ◆ Figure 1). It plays a major role in many fruits and vegetables and is perceived – among others – from OR2J3 [30]. Another example is 3-methyl-butyric acid (19 in ◆ Figure 1), the character impact compound of valerian root [31]. Here, a mutation in the gene for OR11H7P is responsible for the representation of a specific anosmia. For the odorant ß-ionone (20 in ◆ Figure 1), important for the aroma profile of many fruits and fruit juices, a genotype of OR5A1 was also described that accounts for 96 % of the phenotypic sensitivity [32]. Individual (and heritable) manifestations of such kind may impact the elucidation and choice of certain food and food groups.

If an SNP leads to a change in olfactory perception, it may have an impact on the dietary preferences and habits of the mutation's carrier. Insofar the olfactory individuality may be interpreted as genetically manifested dietary preferences.

Evolution and smell

A very exciting question deals with the evolutionary events leading to the common characteristics of our sense of smell and to the respective dietary preferences. Roasted food and roasted meat in particular may serve as an applicable example to discuss these interrelationships. From the paleo-anthropologic view, the controlled and active handling of fire may be seen as a key event in human evolution. Control of fire not only meant to be protected from predator animals, but also opened up the possibility to enhance the nutritive value of food, to reduce its microbiological background, and in turn to increase its storage stability [33, 34]. Along with the roasting of meat, the development of a very specific aroma profile occurs (e.g. pyrroles, pyrazines, and many more), which is perceived as pleasant from a vast majority of customers. The detection of high-quality and safe (in terms of microbiology) food could have been an advantage over individuals not bearing this sensory capability in early stages of mankind.

One important question, however, remains: What developed first? The preference for roasted meat, the control of fire, or the capability to smell odorants specific to roasted meat? These relations between the late development of the human sense of smell and the establishment of the typical human diet might represent a kind of co-evolution within the human species. E.g. a population of humans mastered at controlling fire, and within this population a few individuals were capable to detect (or prefer) roasted meat. A positive selection toward the preference of nutrition relevant odorants could also help to explain why only 2 % of all volatile substances found in food are sufficient to make up the aroma profiles of virtually all foods.

These and many more controversially discussed issues in odor research may one day be answered as a result of collaboration of disciplines such as food chemistry, physiology, genetics, and anthropology.

Conflict of Interest
The authors declare no conflict of interest.

Dr. Matthias Kotthoff
Fraunhofer Institut für Molekularbiologie und Angewandte Oekologie IME
Auf dem Aberg 1, 57392 Schmallenberg
E-Mail: matthias.kotthoff@ime.fraunhofer.de

Svenja Nörenberg
Flavologic GmbH
Dompfaffweg 15, 85591 Vaterstetten

References

1. Dunkel A, Steinhaus M, Kotthoff M et al. (2014) Nature's chemical signatures in human olfaction: a foodborne perspective for future biotechnology. Angew Chem Int Ed Engl 53: 7124–7143
2. Wagner R, Czerny M, Bielohradsky J et al. (1999) Structure-odour-activity relationships of alkylpyrazines. Z Lebensm Unters Forsch 208: 308–316
3. Rothe M, Thomas B (1963) Aromastoffe des Brotes. Z Lebensm Unters Forsch 119: 302–310
4. Guth H (1996) Determination of the configuration of wine lactone. Helv Chim Acta 79: 1559–1571
5. Schwab W (2013) Natural 4-hydroxy-2,5-dimethyl-3(2H)-furanone (Furaneol(R)). Molecules 18: 6936–6951
6. Ubeda C, San-Juan F, Concejero B et al. (2012) Glycosidically bound aroma compounds and impact odorants of four strawberry varieties. J Agric Food Chem 60: 6095–6102
7. Blank I, Schieberle P (1993) Analysis of the seasoning-like flavour substances of a commercial lovage extract (Levisticum officinale Koch.). Flavour Fragr J 8: 191–195
8. Belitz HD, Grosch W, Schieberle P. Lehrbuch der Lebensmittelchemie. 5., vollst. überarb. Aufl., Springer, Berlin (2001)
9. Polster J, Schieberle P (2010) Structure-activity relationships in homologous series of mercaptans: Chemoreception of thiols vs. the corresponding alcohols and thioethers. Abstract of Papers, 238th ACS National Meeting, Washington, DC, United States, August 16–20, 2009, AGFD-189
10. Lorber K, Schieberle P, Buettner A (2014) Influence of the chemical structure on odor qualities and odor thresholds in homologous series of alka-1,5-dien-3-ones, alk-1-en-3-ones, alka-1,5-dien-3-ols, and alk-1-en-3-ols. J Agric Food Chem 62: 1025–1031
11. Polster J, Schieberle P (2015) Structure-odor correlations in homologous series of alkanethiols and attempts to predict odor thresholds by 3D-QSAR studies. J Agric Food Chem 63: 1419–1432
12. Viswaprakash N, Dennis JC, Globa L et al. (2009) Enhancement of odorant-induced responses in olfactory receptor neurons by zinc nanoparticles. Chemical Senses 34: 547–557
13. Wang J, Luthey-Schulten ZA, Suslick KS (2003) Is the olfactory receptor a metalloprotein? Proc Natl Acad Sci U S A 100: 3035–3039
14. Buser HR, Zanier C, Tanner H (1982) Identification of 2,4,6-trichloroanisole as a potent compound causing cork taint in wine. J Agr Food Chem 30: 359–362
15. Bushdid C, Magnasco MO, Vosshall LB et al. (2014) Humans can discriminate more than 1 trillion olfactory stimuli. Science 343: 1370–1372
16. Geithe C, Andersen G, Malki A et al. (2015) A butter aroma recombinate activates human class-I odorant receptors. J Agric Food Chem 63: 9410–9420
17. Schieberle P, Gassenmeier K, Guth H et al. (1993) Character impact odor compounds of different kinds of butter. Lebenson Wiss Technol 26: 347–356
18. Dignum MJW, Kerler J, Verpoorte R (2001) Vanilla production: Technological, chemical, and biosynthetic aspects. Food Rev Int 17: 199–219
19. Egawa T, Kameyama A, Takeuchi H (2006) Structural determination of vanillin, isovanillin and ethylvanillin by means of gas electron diffraction and theoretical calculations. J Mol Struct 794: 92–102
20. Malnic B, Hirono J, Sato T et al. (1999) Combinatorial receptor codes for odors. Cell 96: 713–723
21. Charlier L, Topin J, Ronin C et al. (2012) How broadly tuned olfactory receptors equally recognize their agonists. Human OR1G1 as a test case. Cell Mol Life Sci 69: 4205–4213
22. Noe F, Polster J, Schieberle P et al. (2015) Structure-activity relationships of mercaptans on odorant receptor OR2M3 may explain the characteristic odour threshold trend across a homologous series of 3-mercapto-2-methylalkan-1-ols in humans. Flavour Science: Proceedings of the XIV Weurman Flavour Research Symposium. Context Products Ltd., Leicestershire/U.K. 14: 353–356
23. Weiss T, Snitz K, Yablonka A et al. (2012) Perceptual convergence of multi-component mixtures in olfaction implies an olfactory white. Proc Natl Acad Sci U S A 109: 19959–19964
24. McGorrin RJ. Character impact compounds: flavors and off-flavors in foods. In: Marsili R (Hg). Flavor, fragrance, and odor analysis. Marcel DekkerAG (2002), S. 375–413
25. Everding F (1998) Verpackungsinnovation als Herausforderung für Marketingentscheidungen. Das Beispiel der Mineralwasserbranche zur Entscheidung für das PET 1l-Mehrweggebinde. Diplomarbeit, 128 Seiten, S. 83–84
26. Nijssen B, Kamperman T, Jetten J (1996) Acetaldehyde in mineral water stored in polyethylene terephthalate (PET) bottles: Odour threshold and quantification. Packaging Technology and Science 9: 175–185
27. Strube A (2010) Mineralwasser. Identifizierung des medizinischen Fehlaromas. Dtsch Lebensmitt Rundsch 106: 654–660
28. Schormüller J. Enzyme. Springer Verlag (1965)
29. Keller A, Zhuang H, Chi Q et al. (2007) Genetic variation in a human odorant receptor alters odour perception. Nature 449: 468–472
30. McRae JF, Mainland JD, Jaeger SR et al. (2012) Genetic variation in the odorant receptor OR2J3 is associated with the ability to detect the "grassy" smelling odor, cis-3-hexen-1-ol. Chemical Senses 37: 585–593
31. Menashe I, Abaffy T, Hasin Y et al. (2007) Genetic elucidation of human hyperosmia to isovaleric acid. PLoS Biol 5: e284
32. Jaeger SR, McRae JF, Bava CM et al. (2013) A Mendelian trait for olfactory sensitivity affects odor experience and food selection. Curr Biol 23: 1601–1605
33. Carmody RN, Wrangham RW (2009) Cooking and the human commitment to a high-quality diet. Cold Spring Harb Symp Quant Biol 74: 427–434
34. Smith AR, Carmody RN, Dutton RJ et al. (2015) The significance of cooking for early hominin scavenging. J Hum Evol 84: 62–70

DOI: 10.4455/eu.2016.005