Review

The taste of fat

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ABSTRACT

For many years, fat in meats have been considered to convey quality although variations in the amounts of fat were often poorly correlated with eating qualities. The contribution of fat to taste is equally controversial, because a specific 'fat taste' perception had not been characterized.

The innate attraction for fats may be due to one or more of orosensory, post-ingestive and metabolic signals. This literature review suggests that taste of lipids, particularly of oxidized PUFAs and their esters, may derive from a specific fatty acid perception mechanism in human lingual papillae. Interactions of the CD36 scavenger system with the many compounds derived from fats in cooked and processed meats offer an explanation for the variety of flavors and off-flavors found in meats. The genetic variations in the presence of receptor proteins could be one of the factors related to the differences in fat preferences in different countries and between genders.

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1. Introduction

Fat in meat and meat products is usually associated with high quality and some fat is thought essential for cooking and to maintain good eating quality. However, many consumers also believe that excess fat consumption will increase their risk of cardiovascular diseases. This review looks at 'taste' as a generic term in appreciation and in flavor in relation to recent research into lipid receptor mechanisms, which show that variations in oxidised-lipid binding to lingual receptors may be responsible for some of the differences in appreciation of meat quality.

2. Fat quality and consumer preferences

The evaluation of fat by the consumer comprises elements of the fat itself (its amount and quality), as well as the consumer's sensory capacities, cultural background and concerns about environmental and ethical considerations in meat production. The content and types of fat in meat, in relation to eating quality, have been studied systematically for more than 3 decades as they impact on meat production. They mainly concern variations in 'neutral lipids' as oppose to the phospholipids, present mainly in membranes. The fat content of meat from most species is important in appearance and some research approaches linked intuitively the content of fat with a role in texture, comprising tenderness and juiciness, and in flavor. Because of the concerns over potential health risks from consumption of animal fats, many

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animal production and husbandry methods, such as the production of entire male animals, breeds and crosses and the use of implants, aim at reducing fat content in meats.

The importance of fat content to the appearance and choice of meat is incontrovertible and many reports have shown the relationships in meats from different species. In a recent study of over 12,000 consumers from 23 countries, the amount of pork backfat and colour of the lean were the most important factors, with marbling and drip less important (Fig. 1). The majority of consumers, particularly in Poland, Finland and Mexico, preferred low fat cover. The majority of Irish consumers preferring light red, lean pork, with no marbling and no drip, and Australian consumers, light red, lean pork, again with no marbling. However, many Korean, Japanese and Taiwanese consumers preferred the more marbled and fatter pork. The results of a self-reported questionnaire showed that most socio-economic factors and eating habits were related to choice of subcutaneous fat cover but few factors were common across countries. Gender had the most consistent influence and, in all but one of the countries, a greater proportion of women than men chose the pork with less fat cover (Ngapo, Martin, & Dransfield, 2007b). In beef, the majority of British consumers preferred lean ribs and, from 1982 to 2002, about a quarter of all consumers had shifted their preference towards leaner beef (Ngapo & Dransfield, 2006). The consistency of fatty tissue in pork is also an important quality component and may lead to a soft and unsightly product (Enser, Dransfield, Jolley, Jones, & Leedham, 1984). The ratio of stearic to linoleic acid was the best discriminator of fat firmness in which about half the lipid in pig backfat triglycerides present as linoleic acid (Wood et al., 1978).

In relation to meat production, early American work (Luckett, Bidner, Icaza, & Turner, 1975) showed that 60–70% of consumers who rated rib-eye, found no or slight preference related to marbling and, although lower grading (leaner) carcasses gave less tender meat, it was thought that this was due their more rapid cooling. In another study, conducted over a 3-year period on meat from 500 steers, it was concluded that USDA quality (largely based on differences in fat cover) grades were of minimal value in predicting tenderness (Champion, Crouse, & Dikeman, 1975). In pigs, only about 10% of the variation in tenderness was accounted for by variations in lean or fat content and increases in fat content of pigmeat up to 2.5% increased quality but there was no relationship above this value (Kirkgaard, Moller, & Wismer-Pederson, 1979). In cooked beef, perception of flavor appears to differ across countries, possibly related to the different cooking methods (Dransfield et al., 1984). In sheep fed different dietary oil sources (Nute et al., 2007), lamb flavor was best correlated with phospholipid fatty acid linolenic acid (C18:3n-3) but accounted for only 25% of the variation in sensory ratings.

So, in general, fat content in meats appears to relate strongly to appearance and choice but fat content in raw meats relates weakly to eating quality.

The characteristic meat flavor (see review, Mottram, 1998) is produced during cooking by a complex series of reactions that occur between non-volatile components of lean and fatty tissues. Currently, over 1000 volatile compounds have been identified. Early work suggested that the species differences in flavor are largely explained by differences in lipid-derived volatile components. Several hundred volatile compounds derived from lipid degradation have been found in cooked meat. These include aliphatic hydrocarbons, aldehydes, ketones, alcohols, carboxylic acids and esters. Some aromatic compounds, especially hydrocarbons, have also been reported, as well as oxygenated heterocyclic compounds such as lactones and alkylfurans. In general these compounds result from the oxidation of the fatty acid components of lipids. Exposure to air, storage and heating can cause oxidation of lipid and give rise to 'stale', 'sulphur-rubbery' and 'rancid' off-flavor development including the so-called 'warmed-over flavor' (see review by Byrne & Bredel, 2002). The autoxidation of lipid is the major source of warmed-over-flavor, although reactions involving proteins and heterocyclic compounds may be implicated in the loss of desirable meaty characteristics.

3. Gustatory mechanisms

Gustation (informally often referred to as 'taste' or 'flavor perception') is a form of direct chemoreception in the taste bud that is bathed in saliva and therefore tastant solubility in water will play a role in its perception. The taste bud is composed of sensory taste cells surrounding a central pore, and has several layers of support cells on the outer region of the taste bud (Fig. 2). Taste cells in humans are found on the surface of the tongue, along the soft palate, and in the epithelium of the pharynx and epiglottis (Margolskee, 1993). The superior laryngeal branch of the vagus nerve innovates the epiglottis and larynx and the posterior one-third of the tongue. Different sensory signals from ortho-nasal, retro-nasal odour and gustatory receptors may integrate in the higher centers to give 'flavor' cognition.

There are five well-recognized taste sensations: salty, sour, bitter, sweet and umami and much is now known of the physiology and molecular mechanisms for these basic tastes (for a recent review see: Chandrashakar, Hoon, Ryba, & Zuker, 2006). They are designed to signal both the presence of desirable (salts, carbohydrates and proteins) and harmful (acid and bitter) compounds. Arguably the simplest receptors found in the mouth are the salt (NaCl) and sour (H^+) receptors. An ion channel in the taste cell wall allows ions to enter the cell that causes depolarization of the cell, and opens voltage-regulated Ca^{2+} gates, flooding the cell with ions and leading to neurotransmitter release. The other tastes, bitter sweet and umami involve different G-protein coupled receptor proteins. There are many different classes of bitter compounds and humans can distinguish between the many types of molecule
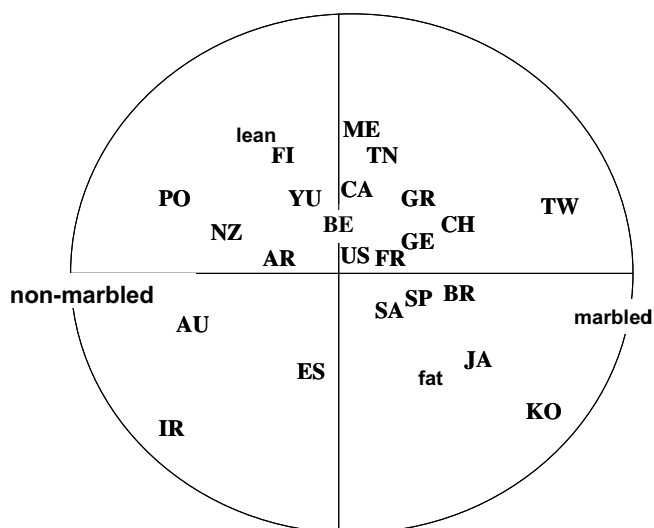

Fig. 1. Fat preferences of different populations. Populations from different countries, a total of 12,590 people from 23 countries, chose photographs of pork chops that had been systematically produced to show variations in fat cover, colour of lean, marbling and drip. The figure shows the relationship (correspondence analysis) between the country and their preference for fat/lean and marbled/non-marbled meat. AU, Australia; AR, Argentina; BE, Belgium; BR, Brazil; CA, Canada; CH, China; ES, Estonia; FI, Finland; FR, France; GE, Germany; GR, Greece; IR, Ireland; JA, Japan; KO, Korea; ME, Mexico; NZ, New Zealand; SA, South Africa; SP, Spain; PO, Poland; TN, The Netherlands; TW, Taiwan; US, United States; YU, Yugoslavia. Adapted from Ngapo, Martin, & Dransfield, 2002, 2007a.
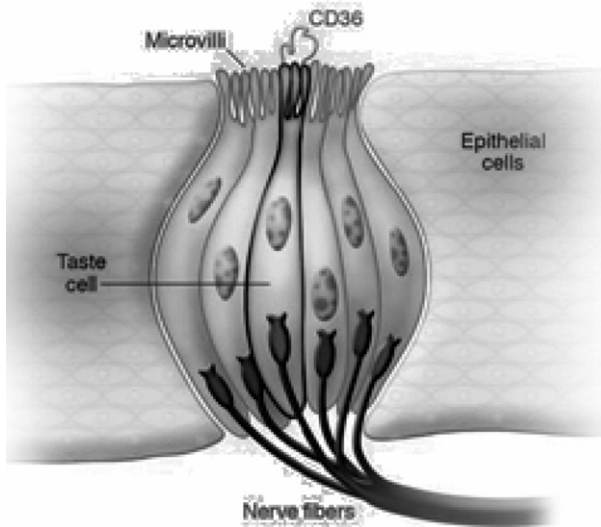
Fig. 2. Stylized representation of a taste bud in the tongue epithelium and the position of CD36 as transmembrane glycoprotein at the apical region of the taste cell.

which produce a generally 'bitter' sensation. Umami (the taste of mono-sodium glutamate, for example) is also described as 'meaty' or 'savory' taste.

Signals from unimodal taste and unimodal olfactory undergo peripheral and central processing to create a flavor percept.

4. Fatty acid taste?

The perception of fats and FAs may be dependent on a combination of textural, olfactory, nociceptive, thermal, and gustatory modalities. Several approaches have been reported to try to determine the existence a specific taste for lipid, particularly by attempting to separate any gustatory effect of lipid from oral texture (viscosity) and odour (including ortho- and retro-nasal) modalities.

In meats, fatty acids are present largely in triglycerides and, in 2003, it was shown (Kawai & Fushiki, 2003) that the addition of a lipase inhibitor diminished the spontaneous preference of rodents for triglycerides but not the preference for free FAs. However, although lipase could release fatty acids from di- or triglycerides in rats, lipase is present only in small amounts human saliva (Gilbertson, Liu, York, & Bray, 1998). So any mechanism for flavor perception in humans is likely to have to take into account di- and triglycerides. In humans, fatty acids with less than 10 carbon chain length may taste sour (e.g., formic and propionic acid; Forss, 1972) and not recognized as fatty. High boiling point lipids are tasteless, probably because of their low water solubility (Forss, 1972). Thermal cooling might contribute to the sensations produced by the melting of fats.

Clinical data have provided some evidence of a taste component of fat perception in humans. Subjects submitted to an oral exposure alone with full-fat food displayed a higher postprandial triglyceridemia than subjects exposed to a fat-free food versions (Mattes, 2001). This metabolic change could not be accounted for by textural and olfactory cues (Mattes, 2005), and it was therefore suggested that an orosensory perception system devoted to lipids could be involved. Consistent with this assumption, healthy subjects seem to be able to detect low quantities of saturated and unsaturated long-chain fatty acids (LCFAs) in a specific manner (Chale-Rush, Burgess, & Mattes, 2007). Orosensory perception is thought to play an important role in the preference for fat-rich

food exhibited both in humans and rodents. Anosmic rats prefer oleate to triolein, so they appear to prefer the taste of fatty acid esters above that of triglycerides without an influence from odour perception (Fukuwatari et al., 2003). In humans (Mattes, 2005), the thresholds for lipids were estimated to be in the mM range for linoleic, oleic and stearic acids and there was no evidence that the degree of saturation affected perception (Alfenas & Mattes, 2003). However, these thresholds seem very high, considering the low concentration (<50 mg/l) of lipids in saliva. By comparing mixtures of basic tastants and linoleic acid, it was concluded that any mechanism for detecting dietary fats was not due to its interference with other tastes (Mattes, 2007).

However, because of the intricate, and often indirect, nature of these sensory and nutritional approaches, the mechanisms underlying lipid flavor perception in humans are controversial.

5. Fatty acid perception

An alternative approach to unraveling the role of fats in perception is to study perception in different organs at the cellular and receptor proteins levels.

In studies of the brain responses to foods and oral chemical stimulation, texture and flavor clues appeared to be spatially separated in the neuron functioning in the brain of the rhesus monkeys (Verhagen, Rolls, & Kadohisa, 2003), although some neurons responded to both texture and flavor stimulations. The primary taste cortex of macaques in the rostral insula and adjoining frontal operculum contains neurons tuned to different tastes and signals are passed to the secondary taste and olfactory cortices, in the orbital frontal cortex (Baylis, Rolls, & Baylis, 1995). Neurons in the secondary taste cortex not only represent taste, but other neurons respond to the oral presence of viscosity, fat texture (Verhagen et al., 2003) or temperature (Kadohisa, Rolls, & Verhagen, 2004). Other neurons respond to combinations of these inputs. The orbitofrontal cortex also contains neurons that respond to olfactory stimuli to form flavor representations (De Araujo, Rolls, Kringelbach, McGlone, & Phillips, 2003). The integration of these different inputs is thought to play a key role in representing the sensory qualities and affective value of food, and thus in the control of eating.

At the cellular level, it has been suggested (Gilbertson et al., 1998) that the mechanism by which taste cells sense dietary fat is by FAs delaying the flux through K^+-channels. This could form a pathway via apical expression of the membrane FA translocase, CD36 (Fig. 2), in taste bud cells (Fukuwatari et al., 2003). However, the time course in humans for activation of the K^+-channel mechanism is slow (Gilbertson et al., 1998) and does not match the rapid
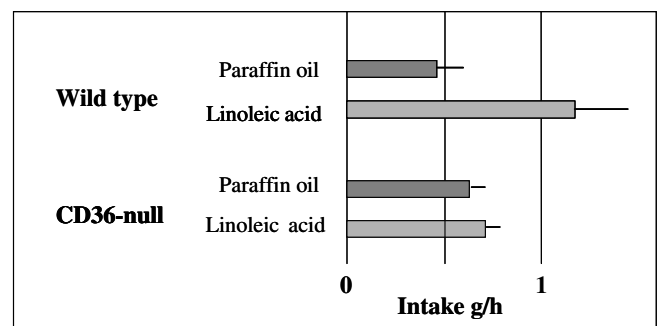

Fig. 3. Intake of lipid-enriched food in wild-type and CD36-null mice. Food intake was measured over 1 h after a 12-h fast from a choice between 5% linoleic acid-, or paraffin oil-, enriched diets in wild-type and knock-out mice. The results show that preference for linoleic acid in the wild-type mice is absent in CD36-deficiency. Bars represent 1 SEM of 12 animals. Data adapted from Laugerette et al., (2005).

sensation of fat in the mouth (Rolls, 1999). More recently (Fig. 3) it was shown in mice that the preference for linoleic acid in feed was abolished in CD36-null mice, providing evidence that CD36 is crucial in oral fat perception and in both metabolic and preference of LCFAs. However, no precautions were taken to reduce oxidation which is likely to have occurred in such food intake studies.

The cluster of differentiation (or CD) is a protocol used for the identification and investigation of cell surface molecules acting as receptors or ligands and CD36, also referred to as fatty acid transporter (FAT), SCARB3, GP88, glycoprotein IV (gpIV) and glycoprotein IIIb (gpIIIb), is an integral membrane protein found on the surface of many cell types, including taste cells (Fig. 2), in vertebrate animals. CD36 is a member of the class B scavenger receptor family of cell surface proteins and binds many ligands including collagen types I and IV, oxidized low-density lipoproteins, native lipoproteins, oxidized phospholipid and long-chain fatty acids. It is a glycoprotein of mass of 76–88 kDa with about 25% (w/w) carbohydrate. Removal of the carbohydrate reduces the mass to about 57 kDa.

CD36 serves as a scavenger and lipid receptor (Silverstein & Febbraio, 2000) and functions in recognition of oxidized lipoproteins, fatty acid transport, cell matrix interactions and anti-angiogenic actions.

In monocytes and macrophages, CD36 activation can be seen as a redistribution from a diffuse pattern with a few small aggregates to larger isolated clusters (McGilvray, Serghides, Kapus, Rotstein, & Kain, 2000). This visualization of the initial activation of CD36 occurs in taste cells exposed to PUFA's. Within the first minute of exposure to linoleic and linolenic acid, large clusters of the receptor are seen in the region of the cell membrane (Fig. 4). Exposure to cholesterol does not induce this ligand-mediated redistribution.

In line with the range of receptor functions, the ligands recognized by CD36 vary considerably in molecular structure. It has been known for a number of years that oxidized forms of low-density lipoproteins, anionic phospolipid (Puente Navaro, Daviet, Ninio, & McGregor, 1996; Ryeom, Silverstein, Scotto, & Sparrow, 1996) and oxidatively fragmented choline (Davies et al., 2001) compounds are ligands for CD36. However, the identification of lipid-derived ligands has proved difficult because of the vast array of lipid oxidation products that can be formed. Using phosphatidylcholine (PC) analogues (Podrez et al., 2002), the biologically active lipid identified (Fig. 5) was a truncated sn-2 fatty acid constituent

Fig. 5. Comparison of ligands from lipid oxidation for CD36 and compound produced in meats. The core structural motif for CD36 binding (top formula, adapted from Podrez et al., 2002) was conserved among various oxidized phospocholine species. A = phospocholine moiety, X = OH or O and Y = OH or H. This is compared to the formulae of some compound influencing the flavor of meats.

possessing α,β-unsaturated γ-hydroxyaldehyde moieties, analogous to 4-hydroxy-2-nonenal (4-HNE). Competitive binding of different oxidation products to CD36 varied more than 50-fold. The 5-hydroxy-8-oxo-6-octenoic acid and 9-hydroxy-12-oxo-10-dodecenoic acid esters were generated during oxidative fragmentation of the PUFA by reactions that alternately liberate aliphatic cleavage products with α,β-unsaturated γ-hydroxyaldehyde moieties as in the formation of 4-HNE. 4-HNE is an aldehyde produced from the oxidation of omega-6-PUFAs and, at higher levels than physiological ones, is considered toxic to mammalian cells.

6. Distribution and expression of CD36 in tissues and populations

CD36 is found on the surface of many different types of cell and is the primary fatty acid transporter in heart and skeletal muscle although the role in liver and adipose tissue may be delegated to other transporters (Luiken et al., 2002). In both human and rat skeletal muscle, the expression of CD36 is higher in type 1 than in type 2 muscle fibers, presumably, because type 1 fibers have a higher fat oxidative potential compared with type 2 fibers (Ibrahimi et al., 1999; Vistisen et al., 2004) correspondingly to their higher requirement for fatty acid uptake.

In view of the differences in fat choices and preferences among consumers in different countries (Fig. 1) and between the genders, it is interesting to note that variations in CD36 and related proteins are also dependent on these factors. The incidence of CD36-deficiency in humans ranges from 0.3% to 18.5% depending on the subpopulation (Aitman et al., 2000; Curtis & Aster, 1996). The lack of these proteins is found in about 0.3% of Caucasians and is more common in African (2.5%), Japanese and other Asian populations (5–11%). The level of CD36 protein in muscle was 49% higher in women than in men (Kiens et al., 2004). It would be interesting to test the relationships between CD36 expression and preference for fat by direct observation.

Other factors may also play a role in preference for lean/fat. Other factors also affect the expression on CD36. The level was dependent on physical training and a 90-min exercise bout induced an increase in CD36 mRNA levels in all groups. Women also have higher muscle mRNA levels of several proteins related to muscle lipid metabolism compared with men. CD36 expression is also dependent on the presence of fatty acid esters. Treatment with 500 μM 1:1 oleate:palmitate for 24 h increased CD36 expression 5-fold and is increased in a dose-dependent manner following treatment (24 h) with insulin. CD36 mRNA expression is also 4-fold
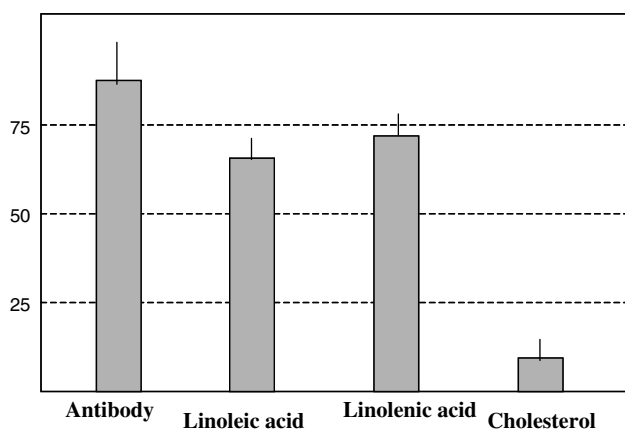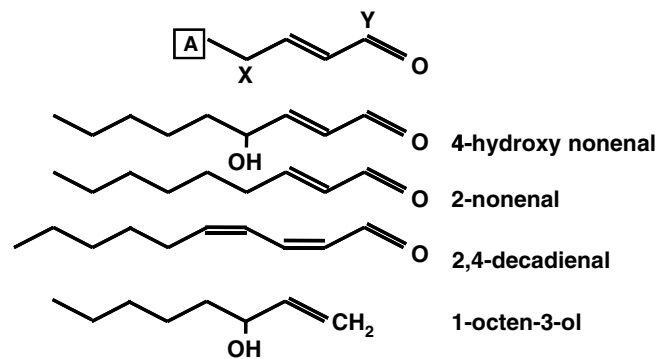

Fig. 4. Clustering of CD36 after stimulation in rat taste buds. Receptor clustering is the first step in CD36 activation and the columns show the extent of clustering of CD36 in rat taste buds after stimulation by added lipids in a buffered solution. The clustering antibody has been added as a positive control. The results show that both linoleic and linolenic acid cause extensive the clustering of CD36 while cholesterol does not. Error bars represent 1 SD from 6 rats. Courtesy of Dr. M.A. Lawson, KVL, Copenhagen.

higher in obese compared to lean muscle cells (Bell, Slentz, Muoio, & Dohm, 2007). The list of factors identified to date is undoubtedly incomplete.

7. Oxidation

Oxidation of lipids in meats is affected by many factors from animal production, meat handling, meat processing and cooking. It has been studied over several decades.

Postmortem factors can influence lipid oxidation and decrease the shelf life of meat products due to the initiation of peroxidation (Vercellotti, St. Angelo, & Spanier, 1992) which, in fatty acids in animal tissues, starts to occur almost instantly after slaughter (Gray & Pearson, 1994). Lipid oxidation is a complex reaction between fatty acids and oxygen in which the initial step in the reaction is the generation of transitory hydroperoxides, which degrade to form a series of secondary products, such as aldehydes, alcohols, acids and ketones which relate to undesirable flavors (Shahidi, 1994). Compounds, such as 2,4-decadienal and 2-nonenal, that are generated by the oxidative degradation of omega-7-unsaturated fatty acids may contribute to the rancid, linseed and cardboard flavors described in meats (Byrne & Bredel, 2002). Storage of cooked beef treated with free-radical scavengers showed more stable beef taste than beef stored alone or with chelator treatment (St. Angelo, Crippen, Dupuy, & James, 1990) showing the importance of lipid autoxidation.

The major unsaturated fatty acids in animals are oleic, linoleic, linolenic and arachidonic acids and autoxidation increased in that order and in fish, poultry, pork, beef, lamb representing increasing levels of unsaturated fatty acids in tissue phospholipids.

Salt, used in many meat products as preservative and tastant, promotes lipid oxidation in pre-cooked meat products but the mechanism is poorly understood (Kanner, 1994).

In dried sausage ripening, lipid oxidation products increased especially towards the end of ripening, with the production of 2-heptanol, 1-octen-3-ol, 2-heptanone and 2-nonanone. Surface moulds probably caused 4-heptanone to appear late in the processing (Sunesen, Dorigoni, Zanardi, & Stahnke, 2001).

It is well recognized that oxidative storage of meats decreases the sensory ratings for normal meaty flavor and increases the ratings of 'off-flavors' and the effect is exacerbated in meat stored under an oxygen-enriched atmosphere (Table 1). Oxidation may lead to the development of warmed-over-flavor, comprising 'rancid' and 'sulphur/rubber' sensory notes (Byrne & Bredel, 2002) and is important to consumer liking (Fig. 6).

The limit of detection of HNE in spiked samples was 0.043 mg/kg and is present in pork products, especially smoked and/or cooked pork (Zanardi, Jagersma, Ghidini, & Chizzolini, 2002).

Table 1
Relationships between ratings of sensory attributes and TBARS in beef

Attribute	Correlation coefficient
Rancidity	+0.84
Abnormal flavour	+0.82
Greasy	+0.70
Metallic	−0.36
Livery	−0.60
Bloody	−0.60
Beef flavor	−0.80

Beef was exposed to treatments (freezing, thawing and storage in high oxygen modified atmosphere packaging) to promote lipid oxidation. TBARS (thiobarbiturate reactive substances) were as high as 12.0. Values are the correlation coefficients between ratings of different attributes and the levels of TBARS. Adapted from Campo et al. (2006).
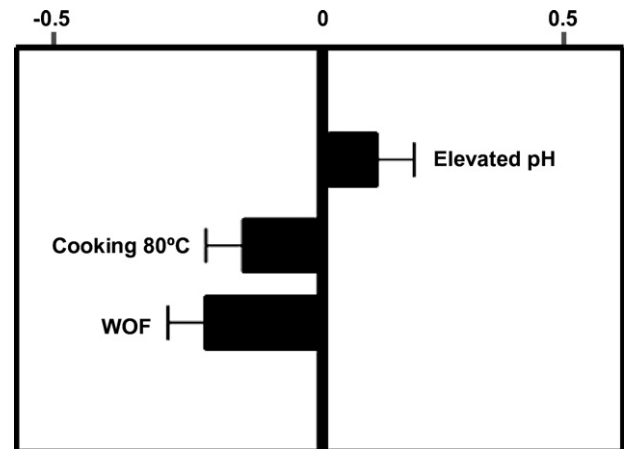

Fig. 6. Warmed-over-flavour contribution to consumer liking. Values are the regression coefficients (error bars 2 standard uncertainties) for the main contributors to liking. The dislike for WOF was the single most important contributor to consumer (dis)liking. Adapted from Bryhni et al., (2003).

So the conclusions reached by some workers in respect of lipid does not rule out an effect due to the presence of small quantities of oxidation products.

In studying the responses to oral administration of lipids in rhesus monkeys, oxidized lipid as the source of sensory perception is consistent with results on the brain neuron functioning in which 'old' vegetable oil caused a much higher response in 'fat and taste' neurons than 'fresh' vegetable oil (Verhagen et al., 2003). Unfortunately, no chemical measurements were given to describe the chemical changes that occurred during storage and, although oxidation would have taken place, other chemical modifications during storage may have been responsible for its higher neuron activity.

8. Conclusions

Employing different approaches of nutrition, sensory evaluation, neurobiology and cell biology in human and laboratory animals from different laboratories have given new insights into the mechanisms involved in taste. By comparing the known scavenger and lipid receptor functions of CD36, based largely on animal models, it appears that humans have a specific sensory system for the detection of the taste of fatty acids. This is in addition to the well-recognized 'five basic tastes'. In particular, sensing their oxidation products of naturally occurring lipids may impact on meat flavors and off-flavors giving rise to a variety of sensory attributes and sensory terms.

Understanding the mechanism of perception of lipids is an important challenge, which may give rise to new approaches for the improvement of animal and human nutrition and in the development of improved meat products.

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