The role of nutrients in meat flavour formation

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The role of meat in the human diet' addresses a very broad subject, covering the nutritional, social, economic and gustatory aspects of meat eating. Although meat is an important source of nutrients, this is probably not the reason why most people eat it; those who eat meat do so because they like the characteristic aroma, flavour and texture. However, the nutritional aspects of meat and its flavour are related, as many of the nutrients in meat are also involved in flavour formation.

Flavour, whether of meat or any other food, comprises mainly the two sensations of taste and smell, although other sensations such as astringency, mouthfeel and juiciness may also play a part. Receptors in the mouth can recognize four main taste sensations (sweet, salt, sour and bitter). In contrast, many hundreds or even thousands of different odours can be distinguished by the human nose. The sensation of odour is produced by volatile chemical substances which stimulate the receptors in the nasal epithelium. Odour compounds may reach these receptors either through the nose (by smelling) or through the posterior nares at the back of the nose and throat while food is being chewed in the mouth. Thus, odour plays a major part in defining the characteristic flavour of a food.

SUBSTANCES IN MEAT RESPONSIBLE FOR TASTE AND ODOUR

While odour is generally caused by low-molecular-weight volatile compounds, taste substances are usually much larger and water soluble. A further class of non-volatile components, known as flavour enhancers, do not necessarily possess a taste or aroma themselves but enhance the flavour of other compounds.

Taste compounds

These are non-volatile or water-soluble compounds with taste or tactile properties, including inorganic salts and sodium salts of certain acids (salty), hypoxanthine, peptides and some amino acids (bitter), sugars and some amino acids (sweet) and acids (sour) (Moody, 1983).

Flavour enhancers

These increase the deliciousness or savouriness of a food (known as 'umami' in Japanese) and include L-amino acids containing five C atoms and certain 5'-nucleotides. The most important flavour enhancers in meat are glutamic acid, monosodium glutamate and inosinic acid (Moody, 1983; Shahidi et al. 1986).
Odour compounds

There are thousands of low-molecular-weight compounds which can give rise to odour sensations; these include both aliphatic and aromatic compounds which generally contain a heteroatom (O, N, S). This confers a precise electronic configuration which is recognizable by the nasal receptors. Such compounds can arise from a variety of sources. In raw fruit and vegetables aroma compounds are formed by enzymic action during ripening. Enzymic action, also, can be responsible for the fermentation of unpleasant odours in meat and other foods, whether due to microbiological spoilage or the metabolism of the animal; off-flavours can also arise due to autoxidation of lipids or external contamination (Saxby, 1993). However, in cooked foods many of the volatile compounds are formed by chemical reactions caused by heating; in the case of cooked meats these reactions are the main source of odour compounds (Mottram, 1991).

While many of the taste compounds also have a nutritional function, aroma compounds have almost no nutritional value as only very low quantities are present in meat. However, these aroma compounds are formed by reactions occurring during the cooking process and most of the precursors of these reactions are nutritional components of meat.

More than 800 volatile compounds have been identified in cooked beef aroma (Maarse, 1989). However, it is believed that a relatively small number of compounds actually play an important part in the overall aroma of cooked meat. Whether a compound is one of these key odour impact compounds depends on both its concentration and its odour threshold, i.e. how sensitive the human nose is to that particular compound. Table 1 lists some of the most important aroma compounds in cooked beef; individually, they have odours as shown, but together they give cooked beef aroma. Probable routes of formation of these compounds are also given: trans-2-nonenal, trans,trans-2,4-decadienal and 1-octen-3-one may be derived from the thermal oxidation of polyunsaturated fatty acids; methional, phenylacetaldehyde and 2-acetyl-1-pyrroline are products of the Maillard reaction between amino acids and reducing sugars (the first

<table>
<thead>
<tr>
<th>Compound</th>
<th>Odour</th>
<th>Precursor(s)</th>
<th>Mechanism</th>
</tr>
</thead>
<tbody>
<tr>
<td>Trans-2-nonenal*</td>
<td>Tallowy, fatty</td>
<td>n-6 Fatty acids</td>
<td>Thermal oxidation</td>
</tr>
<tr>
<td>Trans,trans-2,4-decadienal†</td>
<td>Fatty, fried potato</td>
<td>n-6 Fatty acids</td>
<td>Thermal oxidation</td>
</tr>
<tr>
<td>1-Octen-3-one*</td>
<td>Mushrooms</td>
<td>n-6 Fatty acids</td>
<td>Thermal oxidation</td>
</tr>
<tr>
<td>2-Acetyl-1-pyrroline*</td>
<td>Roasty, sweet</td>
<td>Proline†</td>
<td>Maillard reaction</td>
</tr>
<tr>
<td>Methional*</td>
<td>Cooked potato</td>
<td>Methionine</td>
<td>Strecker degradation</td>
</tr>
<tr>
<td>Phenylacetaldehyde*</td>
<td>Honey-like, sweet</td>
<td>Phenylalanine</td>
<td>Strecker degradation</td>
</tr>
<tr>
<td>2-Methyl-3-furanthiol*</td>
<td>Meat-like, sweet, sulphurous</td>
<td>Cysteine and ribose or Thiamin</td>
<td>Maillard reaction</td>
</tr>
<tr>
<td>Bis 2-methyl-3-furyl disulphide*‡</td>
<td>Meat-like, o xo</td>
<td>Thiamin</td>
<td>Thermal degradation</td>
</tr>
<tr>
<td>2-Methyl-3-furyl 2-furfuryl disulphide‡</td>
<td>Roasted, meat-like</td>
<td></td>
<td></td>
</tr>
<tr>
<td>β-Ionone*</td>
<td>Violet-like</td>
<td>β-Carotene</td>
<td>Oxidative degradation</td>
</tr>
</tbody>
</table>

* Gasser & Grosch (1988).
† Grosch & Schieberle (1991).
two are formed by the Strecker degradation of the amino acids methionine and phenylalanine respectively; β-ionone is probably formed from the oxidative breakdown of β-carotene from the diet (Gasser & Grosch, 1988). The furyl disulphides can be formed either by the Maillard reaction between cysteine and reducing sugars or from the breakdown of thiamin (vitamin B₁); these compounds will be discussed in more detail in the following section.

While there are aspects of the formation of these compounds which remain unclear, it is apparent that two reactions are of particular importance in meat aroma formation: the Maillard reaction and the oxidation of lipids during heating.

**THE MAILLARD REACTION BETWEEN SUGARS AND AMINO ACIDS**

The Maillard reaction between amino acids (or peptides) and reducing sugars is important for flavour formation in many cooked foods. This reaction is a complex network of reactions which yields both high-molecular-weight brown-coloured products and volatile aroma compounds. The Maillard reaction has been extensively reviewed (for example, see Hurrell, 1982). The reaction between one amino acid and one sugar will yield hundreds of volatile compounds (Salter et al. 1988; Farmer et al. 1989). These include a range of heterocyclic compounds, in which a ring structure contains an atom of N, O or S, depending on the heteroatoms present in the amino acid. The odour obtained from such reactions is also dependent on the amino acid, while the nature of the sugar dictates the rate of the reaction (Kiely et al. 1960). In the case of cooked meat, the S-containing amino acids have particular relevance, especially cysteine (Kiely et al. 1960; Morton et al. 1960). Reactions of this type have been patented for use as synthetic meat flavourings (MacLeod & Seyyedain-Ardibili, 1981).

The compounds found to be of particular importance for artificial ‘meaty’ flavours are the furan and thiophene thiols and disulphides (MacLeod, 1986). They have in common a furan or thiophene ring with a thiol group in the 3-position; this gives a ‘meaty’ aroma, while similar compounds with a thiol in the 2-position tend to be ‘burnt’ and ‘sulphurous’. The best meat-like aroma is given when there is a methyl group adjacent to the thiol group and the ring contains at least one double bond (van den Ouweland et al. 1989). A number of compounds of this type have now been identified in cooked meats (Gasser & Grosch, 1988, 1990; Farmer & Patterson, 1991; Mottram & Madruga, 1993). The use of odour dilution techniques has demonstrated that 2-methyl-3-furanthiol, bis 2-methyl-3-furyl disulphide and 2-methyl-3-furyl 2-furfuryl disulphide are among the most important contributors to beef flavour while 2-methyl-3-furanthiol and 2,5-dimethyl-3-furanthiol are important odour compounds in chicken (Fig. 1). The formation of some of these compounds has been shown to depend on pH and this may explain the known pH dependency of meat flavour (Farmer & Mottram, 1990b).

Furanthiols and their disulphides can be formed from either the Maillard reaction between cysteine and a reducing sugar (Farmer et al. 1989; Farmer & Mottram, 1990b) or from the thermal degradation of thiamin (van den Ouweland & Peer, 1975). Which of these mechanisms is most important in meat itself remains the subject of research (Grosch et al. 1993; Mottram & Madruga, 1993). In model systems, both the Maillard reaction and the breakdown of thiamin produce a wide range of odorous compounds (MacLeod & Seyyedain-Ardibili, 1981; Mottram, 1991).
LIPID OXIDATION

Lipids can break down via oxidation of the fatty acids to give volatile odour compounds which contribute to both desirable and undesirable flavours (Mottram, 1987). At room temperature and even, to a lesser extent, at refrigeration and freezer temperatures, autoxidation of lipids can occur to give rancidity in raw meat or ‘warmed-over flavour’ in stored cooked meat. However, the heating of lipids (as in cooking) gives rise to thermal oxidation reactions which, although they follow very similar pathways to autoxidation, give slightly different products and contribute to the desirable flavour formed during cooking; the balance between the many pathways which make up lipid oxidation is affected by the application of heat.

The oxidation of lipids gives a wide range of aliphatic products, including both saturated and unsaturated hydrocarbons, alcohols, aldehydes, ketones, acids and esters as well as some cyclic compounds (such as furans, lactones and cyclic ketones). Many of these possess intense odours and contribute to the overall aromas of many different kinds of foods (Forss, 1972).

Polyunsaturated fatty acids are much more susceptible to oxidation than mono-unsaturated or saturated fatty acids and some of the key odour impact compounds in meat are derived from polyunsaturated fatty acids (Gasser & Grosch, 1988). Of the different classes of lipids present in meat, phospholipids have a high level of unsaturation and so are particularly vulnerable to oxidation. It is thought that the oxidation of phospholipids is not only important for ‘warmed-over flavour’ but that they also play a significant part in the formation of desirable meat flavour. Evidence for this was obtained by extracting either the triacylglycerols only, or the total lipids (including the phospholipids), from meat (Mottram & Edwards, 1983). A study of the aroma volatiles showed that removal of the triacylglycerols had little effect on either the aroma of the cooked meat or on the pattern of volatile compounds observed using GLC–mass

Fig. 1. Furanthiols and disulphides important in meat flavour: (A), 2-methyl-3-furanthiol; (B), bis 2-methyl-3-furyl disulphide; (C), 2,5-dimethyl-3-furanthiol; (D), 2-methyl-3-furyl 2-furfuryl disulphide.
spectrometry. However, when the phospholipids were removed as well, the ‘meaty’ character of the aroma was lost and there was a marked alteration in the volatile products. It appeared that phospholipids (but not triacylglycerols) were important for meat flavour formation. In addition, the nature of the changes in volatile compounds suggested that the route by which phospholipids promote meat flavour may involve their participation in the Maillard reaction.

Further work confirmed these effects using model systems (Whitfield et al. 1988; Farmer & Mottram, 1990a). The exact mechanism by which phospholipids improve meaty aroma is not yet known, but it has been established that lipid oxidation and the Maillard reaction do not occur in isolation and that interactions between these two pathways can cause a wide range of effects on the volatile aroma compounds produced (Farmer & Mottram, 1990a, 1992, 1993). The presence of amino acids and sugars can reduce the amounts of potent odorous products of the lipid oxidation reactions, and the presence of lipids can likewise reduce the quantities of some Maillard products. In addition, the interaction of these two reactions also gives a new range of aroma compounds which depend on both reactions for their formation. Thus, an alteration to one precursor can affect the products of several reaction pathways. For example, the level of unsaturation of fatty acids and the precise structures of phospholipids have a large effect not only on the products of lipid oxidation but also on the way that these components affect the Maillard reaction (Farmer & Mottram, 1993).

One example of a link between lipid composition and flavour is that of grass-fed v. concentrate-fed beef. It has been suggested that the flavour of concentrate-fed beef is preferred, with the flavour of grass-fed beef having ‘milky’, ‘grassy’ notes (Melton et al. 1982; Melton, 1983). Compared with grass-fed beef, phospholipids from grain-fed cattle contain more n-6 fatty acids and less n-3 fatty acids; this is thought to be due to the high content of n-3 fatty acids in forage grasses, whereas maize contains high levels of n-6 fatty acids (Melton, 1983; Marmer et al. 1984). These classes of fatty acids give different oxidation products as a result of the different positions of their double bonds; as they are polyunsaturated they are also very reactive for flavour formation. Grass-fed beef has higher levels of low-molecular-weight aldehydes (Larick & Turner, 1990) and some of these possess ‘grassy’ odours; these compounds may arise from thermal oxidation of the n-3 fatty acids. This suggests that the balance of n-6 and n-3 fatty acids in the phospholipids is important for flavour formation.

The characteristic flavours of different species’ meats are also thought to be related to lipid composition. Lamb, pork, chicken and beef have more or less clearly distinguishable aromas. The compounds responsible for these characteristic species notes are not all known. However, those that are known appear to be lipid-derived. For example, in chicken, trans,trans-2,4-decadienal is thought to give the characteristic species note (Pippen & Nonaka, 1960; Gasser & Grosch, 1990), while for lamb various branched-chain fatty acids confer the characteristic flavour (Wong et al. 1975). For beef, recent work has suggested that a branched-chain aldehyde (12-methyltridecanal) derived from the plasmalogen forms of phospholipids may be important (Grosch et al. 1993).

Not only can the precise composition of lipids affect the formation of aroma compounds but so can any meat component capable of influencing the progress of lipid oxidation reactions. For example, vitamin E, which is present naturally in meat, has an antioxidative effect. Morrissey (1993) has described how alterations in the levels of vitamin E affect the development of rancidity in uncooked meat and there is some
evidence that such substances may also affect the formation of aroma compounds during cooking (Laksesvela, 1960). This is an area which requires further attention.

The presence of metal ions, on the other hand, can promote these lipid oxidation reactions and a great deal of work has been done on the effect of Fe$^{3+}$ and haem groups on the formation of 'warmed-over flavour' (Rhee, 1988) and there is some evidence that Cu$^{2+}$ may affect the formation of lipid oxidation products in cooked chicken (Ishida & Kaji, 1981).

**CONCLUSION**

Substances in raw meat of particular importance for flavour-forming reactions during cooking include free amino acids, peptides, sugars and also phospholipids and their fatty acids, while various vitamins and minerals can alter the rate and extent of these reactions. The amounts and proportions of these compounds will dictate the progress of flavour-forming reactions and, hence, the ultimate flavour of the cooked meat. In addition, salts, acids, sugars and other soluble substances contribute to the taste of the meat. Thus, any change in the composition of nutrients in meat (or any other food) could lead to a change in the balance of flavour-forming reactions occurring and, therefore, to a change in the overall aroma and flavour.

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