

Contents

Contributors	xii
Preface	xv
1 Measuring proximal stimuli involved in flavour perception	1
ANDREW J. TAYLOR and JOANNE HORT	
1.1 Factors influencing flavour perception	1
1.1.1 Perception of 'taste' and its location	1
1.1.2 Multimodal nature of flavour perception	2
1.1.3 Distal and proximal stimuli	4
1.2 Aroma	4
1.2.1 Measurement of orthonasal proximal stimuli	5
1.2.2 Measurement of retronasal proximal stimuli	6
1.2.3 Examples of differences in distal and proximal aroma stimuli	10
1.2.4 Relating proximal aroma stimuli to flavour perception	11
1.3 Taste	14
1.4 Texture	18
1.5 Colour and appearance	22
1.5.1 Colour perception	23
1.5.2 Specifying colour	24
1.5.3 Instrumental measurement of colour	27
1.6 Methods to study and quantify crossmodal interactions	29
1.7 Conclusion	34
2 The role of oral processing in flavour perception	39
JON F. PRINZ and RENE DE WIJK	
2.1 Introduction	39
2.2 Anatomy of the peri-oral structures	41
2.2.1 Saliva	44
2.3 Flavour	46
2.4 Oral processing	47
2.5 Conclusion	53

3	The cellular basis of flavour perception: taste and aroma	57
	NANCY E. RAWSON and XIA LI	
3.1	Introduction	57
3.2	Taste and flavour	57
3.2.1	Taste buds and taste cells	58
3.2.2	Molecular mechanisms	60
3.2.3	Salt taste	60
3.2.4	Sour taste	62
3.2.5	Sweet taste	63
3.2.6	Bitter taste	64
3.2.7	Umami taste	64
3.2.8	Individual variations – polymorphisms in receptors	66
3.3	Perception of aroma	67
3.3.1	What is the ‘signal’?	67
3.3.2	How is odorant information encoded?	69
3.3.3	Odour intensity and quality coding in the olfactory bulb	70
3.4	Flavour perception can be modulated: adaptation, sensitisation and crosstalk	74
3.5	Flavour perception and ageing	76
3.5.1	Anatomy and physiology	76
3.5.2	Taste	77
3.5.3	Olfaction	78
3.6	Conclusion	79
4	Structural recognition between odorants, olfactory-binding proteins and olfactory receptors – first events in odour coding	86
	JEAN-CLAUDE PERNOLLET and LOÏC BRIAND	
4.1	Introduction	86
4.2	Anatomy of the olfactory system	89
4.3	Olfactory-binding proteins	90
4.3.1	OBP discovery	90
4.3.2	General properties of vertebrate OBPs	91
4.3.2.1	Structural properties of OBPs	91
4.3.2.2	Comparison with insect OBPs	95
4.3.3	Experimental approaches to OBP–odorant interactions	96
4.3.4	Human OBPs	97
4.3.5	Structure of the odorant-binding pocket	98
4.3.5.1	Crystallographic observations of complexes of OBPs with odorants	99
4.3.5.2	Biochemical molecular modelling and docking investigation of hOBP	99

4.3.6	Potential role of OBPs in odour discrimination	100
4.3.7	Conclusions about OBP	102
4.3.7.1	Vertebrate OBP definition	102
4.3.7.2	Comparison of OBP numbers in vertebrates and in insects and OBP role in odorant discrimination	102
4.3.7.3	Biological role of OBPs	102
4.3.7.4	Putative roles of OBPs	103
4.3.7.5	Lipocalins potentially involved in taste	104
4.4	Olfactory receptors	104
4.4.1	Discovery of ORs as G protein-coupled receptors	104
4.4.1.1	General properties of GPCRs	105
4.4.1.2	GPCR classification	106
4.4.1.3	G proteins as transducers	108
4.4.2	Peculiar properties of ORs	110
4.4.2.1	The second external loop of ORs	110
4.4.3	Odorant recognition by ORs: structural relationships between OR and odorant	112
4.4.3.1	Experimental studies of odorant-OR interactions	112
4.4.3.2	OR functional studies reveal broad odorant selectivity	114
4.4.4	Odorant-binding site in the receptor transmembrane bundle	118
4.4.5	Conclusions on the odorant-OR structural relationships and odotope definition	120
4.4.6	OR classification and genome comparison	121
4.4.6.1	Classification of the OR gene family	121
4.4.6.2	OR nomenclature	122
4.4.6.3	Variability of ORs within the human species	123
4.4.6.4	Comparison of the OR number between man and animal and between vertebrates and insects	123
4.4.6.5	Human OR genome compared to macrosmatic animals	124
4.4.7	Other possible functions for ORs	125
4.4.8	Concluding remarks about ORs	126
4.5	Biochemical mechanisms involved in odorant capture	127
4.5.1	Interactions of OBP with OR	127
4.5.2	Signal transduction in olfactory neurons and neural impulse formation	129
4.5.2.1	Receptor activation and downstream signalling	130
4.5.2.2	OR desensitisation	130
4.5.3	Beyond the olfactory neuron	131

4.6	Conclusion	132
4.6.1	Complexity of stereochemical odorant recognition and subsequent odour coding	132
4.6.2	Taste and VNO receptors compared to ORs	134
4.6.3	Comparison of human and animal olfactory systems	135
4.6.4	Inferences from the recent knowledge about olfaction pericellular events and future progresses	136
4.6.4.1	Odotope mixture cannot be distinguished from odorant mixture	136
4.6.4.2	Human individual variability	137
4.6.5	Olfactory biosensors	138
5	Oral chemesthesis: an integral component of flavour	151
	BARRY G. GREEN	
5.1	Overview	151
5.2	Introduction	151
5.3	The neurophysiological basis of oral chemesthesis	152
5.4	Psychophysical characteristics	155
5.4.1	Sensation quality	155
5.4.2	Spatial factors in sensitivity and sensation quality	156
5.5	The roles of sensitisation and desensitisation in chemesthetic perception	158
5.6	Temperature and chemesthesis	161
5.7	Interactions with touch	162
5.8	Interactions with taste and smell	162
5.9	Individual differences	165
6	Flavour perception and the learning of food preferences	172
	ANTHONY A. BLAKE	
6.1	Introduction	172
6.2	Flavour as an example of molecular communication	173
6.2.1	The human brain	174
6.2.2	Multisensory perception	176
6.3	What flavour is and how we learn to like it	177
6.3.1	Learning to like flavour	183
6.3.2	Flavour learning in adults	191
6.4	Conclusion	197

7	Functional magnetic resonance imaging of human olfaction	203
	MARTIN WIESMANN, BIRGIT KETTENMANN and GERD KOBAL	
7.1	Introduction	203
7.2	The methodological basis of functional magnetic resonance imaging	203
7.2.1	Magnetic resonance imaging	203
7.2.2	Functional magnetic resonance imaging	204
7.2.2.1	Exogenous contrast agent injection	205
7.2.2.2	Arterial spin labelling	205
7.2.2.3	Blood oxygen level-dependent fMRI	205
7.3	fMRI and perception of odorous compounds	208
7.3.1	Anatomy and organisation of the olfactory system	209
7.3.1.1	Olfactory receptors, olfactory nerves and olfactory bulb	210
7.3.1.2	Olfactory tract and primary olfactory cortex	211
7.3.2	fMRI studies of the primary olfactory cortex	213
7.3.2.1	Secondary olfactory regions	215
7.3.2.2	Orbitofrontal cortex	216
7.3.2.3	The role of the amygdala in hedonic processing of odours	218
7.3.2.4	Other brain regions	220
7.3.2.5	Cingulate	220
7.3.2.6	Cerebellum	220
7.3.2.7	Imagination of odours and memory	221
7.4	Interaction between olfaction and other sensory modalities	221
7.4.1	Transduction of pheromone-like compounds in humans	222
7.5	Conclusion	222
8	Flavor interactions at the sensory level	228
	RUSSELL S. J. KEAST, PAMELA H. DALTON and PAUL A. S. BRESLIN	
8.1	Introduction	228
8.2	The psychophysical curve: physical intensity vs. perceived intensity	228
8.3	Attributes of sensory modalities	234
8.3.1	Quality	234
8.3.2	Intensity	234
8.3.3	Temporal pattern	235
8.3.4	Spatial pattern	236

8.4	Adaptation	237
8.5	Four levels of flavor interactions	237
8.5.1	Physiochemical interactions	237
8.5.2	Mechanical/structural interactions	238
8.5.3	Oral and nasal peripheral interactions	238
8.5.4	Central cognitive interactions	239
8.6	Intramodal interactions	239
8.6.1	Taste	239
8.6.1.1	Single-quality interactions	240
8.6.1.2	Multiple-quality interactions	241
8.6.2	Odor	241
8.6.2.1	Odor interactions	242
8.6.3	Somatosensations are components of flavor	242
8.6.3.1	Chemesthesis: irritation	243
8.7	Texture	244
8.7.1	Visual texture	245
8.7.2	Auditory texture	245
8.7.3	Tactile texture	245
8.8	Interactions between modalities	246
8.8.1	Interactions of orosensory chemesthesis, tactile sensations and taste	246
8.8.2	Interactions of odor and somatosensations	247
8.8.3	Interactions of odor and taste	247
8.9	Sources of error in sensory research	248
8.9.1	Individual variation	248
8.9.2	Experimental protocol	248
8.9.3	Choice of flavor-active compound	249
8.9.4	Psychophysical function of a compound	249
8.9.5	Method of rating	249
8.10	Practical implications for flavor	249
9	Psychological processes in flavour perception	256
	JOHN PRESCOTT	
9.1	Flavour as sensory integration	256
9.2	Qualitative and psychophysical evidence for odour–taste integration	257
9.2.1	Taste properties of odours	258
9.2.2	How do taste-related odour qualities develop?	258
9.2.3	How ‘real’ are smelled taste qualities?	259
9.2.4	Influence of smelled taste qualities on the perception of tastes	261

9.3	Smelled taste qualities and taste modification as indicators of flavour formation	263
9.3.1	The role of spatial and temporal factors in odour–taste integration	266
9.4	Cognitive processes in the development of flavour perception	267
9.4.1	Taste modification by odours: a rating effect?	267
9.4.2	Taste modification by odours as a function of perceptual strategy	268
9.4.3	Analysis and synthesis in the perception of flavour	269
9.4.4	Investigating cognitive processes in flavour perception	270
9.5	Implications and future directions	273
9.6	Conclusion	274
	Index	279