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# Fish Chemoreception

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*Chapter nine*

# *Teleost gustation*

Takayuki Marui and John Caprio

## 9.1 INTRODUCTION

Vertebrates, including fishes, possess two principal chemoreceptive systems, termed olfaction and gustation (taste), which are adapted to respond to specific chemical substances in the environment. In all vertebrates, chemical information that is detected and transmitted directly to the central nervous system (CNS) by bipolar neurones of cranial nerve I is termed olfaction, whereas chemical information detected by specialized epithelial cells (i.e. taste cells) and transmitted to the CNS by neurones of cranial nerve VII (facial), IX (glossopharyngeal) or X (vagus) is termed gustation. Receptor cells of both systems are required to discriminate relevant chemical stimuli from background chemical 'noise' existing in the environment of all organisms. Receptor molecules (most probably glycoproteins) that detect and preferentially pass biologically important information have evolved and have been positioned in the membranes of the receptor cells. These receptor molecules, upon being activated by their specific stimulus or stimuli, initiate a series of cellular molecular events that can result eventually in behavioural responses, such as food search and ingestion. Because both olfactory and gustatory systems in fishes are activated by water-soluble substances, it is often difficult to determine the specific role that each system plays in a particular behaviour; this difficulty adds to the confusion of taste/smell distinctions in fish. The present interpretation is that gustation is involved in the detection, selection and ingestion of food and protection against noxious (i.e. generally bitter) substances, and olfaction is involved in a generalized alerting response and is involved in possible specific pheromonal responses associated with fright, mating, spawning, territorial and homing behaviours.

Of the relatively few species of fishes studied with respect to their chemical senses, the Cyprinidae and Siluridae (including Ictaluridae) evolved some of the more highly developed taste systems of all vertebrates. Over the past 20

years, electrophysiological, biochemical and behavioural experiments clearly indicated that rather simple chemical compounds (e.g. amino acids and nucleotides) are particularly stimulatory to the chemosensory systems and appear to play important roles in inducing feeding in a number of aquatic organisms.

This chapter will focus on the physiology of the peripheral taste neurones in teleosts. For recent information on the molecular mechanisms of taste receptor transduction in teleosts see Brand and Bruch, Chapter 7 herein. The organization of gustatory neural pathways within the central nervous system of teleosts is reviewed by Kanwal and Finger, Chapter 5 herein.

## 9.2 HISTORICAL BACKGROUND OF GUSTATORY PERIPHERAL NERVE PHYSIOLOGY

The first electrophysiological recordings of taste activity in a teleost was obtained in an isolated head preparation from the facial/trigeminal nerve complex innervating the barbel of the North American bullhead catfish, *Ictalurus nebulosus* (formerly *Amiurus nebulosus*) (Hoagland, 1933). In this study, acetic acid, sodium chloride and meat juice evoked small potentials in the barbel nerve, whereas mechanoreceptive activity was appreciable. Since this pioneer work, a number of reports concerning the physiology of the taste system of teleosts have appeared (reviews: Bardach and Atema, 1971; Tucker, 1983; Caprio, 1982, 1984, 1988). For studies prior to the middle 1970s, most investigations of fish taste physiology utilized as test stimuli the four classical taste stimuli (sodium chloride, quinine hydrochloride, sucrose and a mineral or organic acid) used in tetrapods. The first investigation to suggest that the fish taste system is highly responsive to particular organic chemicals was performed by Konishi *et al.* (1966). They analysed single fibre activity of taste neurones in the sea catfish, *Plotosus lineatus* (formerly *P. anguillaris*) and found that some of the fibres that were not very responsive to the classical taste stimuli responded well to nereid worm extract, blood sera, human saliva, lecithin and betaine. This result suggested the existence of different fibre types based on chemical specificity. Bardach *et al.* (1967) examined the facial taste system of bullhead catfish (the yellow bullhead, *Ictalurus natalis*, and the brown bullhead, *I. nebulosus*) and tomcod, *Microgadus tomcod*, and indicated that amino acids were effective gustatory stimuli. A critical finding that olfactory receptors of Atlantic salmon, *Salmo salar* (Sutterlin and Sutterlin, 1971) and the white catfish, *I. catus* (Suzuki and Tucker, 1971) were highly sensitive to specific amino acids (estimated thresholds for the more stimulatory compounds ranged between $10^{-7}$ M and $10^{-9}$ M) was the additional impetus that resulted in the finding that facially innervated taste receptors on the maxillary barbel of the channel catfish, *I. punctatus*, were also highly sensitive (estimated thresholds $\leqslant 10^{-9}$ M) to specific amino acid stimuli



(Caprio, 1975, 1978). Subsequently, amino acids were shown to be potent stimuli to the facial taste systems of other species of teleosts (Fig. 9.1), although the taste specificities across the species could be very different (Table 9.1).

Although taste buds innervated by the facial nerve in catfish are broadly distributed, such that they are found within the rostral oral cavity, on the lips, barbels and flank, the sensitivities and specificities of these taste buds for amino acids are similar (Caprio, 1975, 1978; Davenport and Caprio, 1982; Kanwal *et al.*, 1987). The oropharyngeal taste buds innervated by the glossopharyngeal and vagal nerves, although shown to have similar amino acid specificities, were generally less sensitive to specific amino acids by at least 1.5 to greater than 2 orders of magnitude than were facially innervated taste buds (Kanwal and Caprio, 1983). Thus, irrespective of the location of amino-acid-sensitive taste buds, the L-isomers of alanine and arginine are

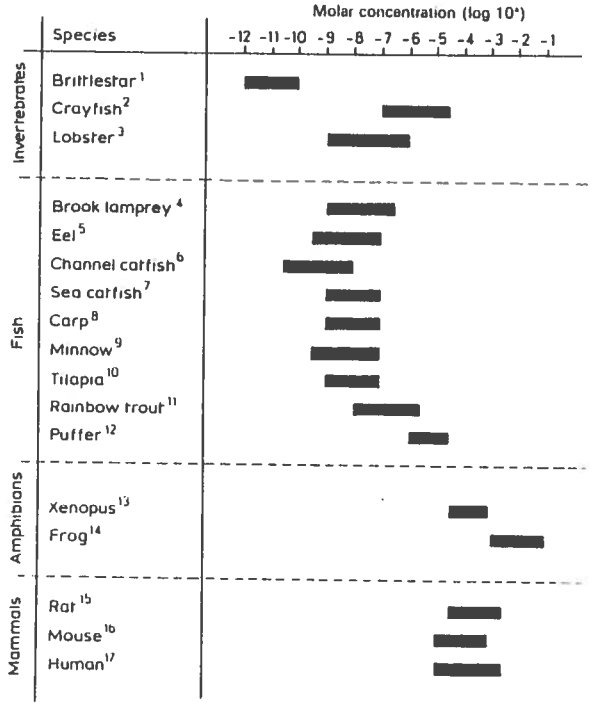


Fig. 9.1 Ranges of taste thresholds for the more potent amino acids, obtained electrophysiologically. Sources: 1, Moore and Cobb (1985); 2, Hatt (1984); 3, Derby and Atema (1982a); 4, Baatrup (1985); 5, Yoshii *et al.* (1979); 6, Caprio (1975); 7, Kohbara (unpublished); 8, Marui *et al.* (1983a); 9, Kiyohara *et al.* (1981); 10, Marui (unpublished); 11, Marui *et al.* (1983b); 12, Kiyohara *et al.* (1975); 13, Yoshii *et al.* (1982); 14, Gordon and Caprio (1985); 15, Harada *et al.* (1983); 16, Harada *et al.* (1982, 1983); 17, Schiffman *et al.* (1981).

Table 9.1 Grouping of fish according to the specificity of gustatory responses to amino acids*

| *Species* | *Stimulatory amino acids†* | *Concentration tested (mM)* | *Source* |
|---|---|---|---|
| | Wide response range | | |
| Channel catfish, *Ictalurus punctatus* | Neutral, basic, and acidic | 0.1 | Caprio (1975, 1978), Davenport and Caprio (1982), Kanwal and Caprio (1983) |
| Topmouth minnow, *Pseudorasbora parva* | Neutral, basic, and acidic | 1.0 | Kiyohara *et al.* (1981) |
| Tiger fish, *Therapon oxyrhynchus* | Neutral, basic, and acidic | 0.1 | Hidaka and Ishida (1985) |
| Rabbitfish, *Siganus fuscescens* | Neutral, basic, and acidic | 0.1 | Ishida and Hidaka (1987) |
| African cichlids, *Tilapia nilotica* | Neutral, basic, and acidic | 1.0 | Marui (unpublished) |
| Red sea bream, *Chrysophrys major* | Neutral and basic | 10.0 | Goh and Tamura (1980a) |
| Mullet, *Mugil cephalus* | Neutral and basic | 10.0 | Goh and Tamura (1980a) |
| Isaki grunt, *Parapristipoma trilineatum* | Neutral and basic | 0.1 | Ishida and Hidaka (1987) |
| Jack mackerel, *Trachurus japonicus* | Neutral and basic | 10.0 | Ishida and Hidaka (1987) |
| Chub mackerel, *Scomber japonicus* | Neutral and basic | 10.0 | Ishida and Hidaka (1987) |
| | Limited response range | | |
| Japanese eel, *Anguilla japonica* | Arg, Gly, Ala, Pro, Lys Ser | 0.1 | Yoshii *et al.* (1979) |
| Rainbow trout, *Oncorhynchus mykiss‡* | AGPA, Pro, Hpr, Bet, Leu, Ala, Phe | 1.0 | Marui *et al.* (1983b) |
| Common carp, *Cyprinus carpio* | Pro, Ala, CysH, Glu, Bet, Gly | 1.0 | Marui *et al.*, (1983a) |
| Arctic charr, *Salvelinus alpinus* | Pro, Hpr, Ala, AGPA | 1.0 | Hara (pers. comm.) |
| Brook trout, *Salvelinus fontinalis* | Pro, Hpr, Ala, Phe, AGPA | 1.0 | Hara (pers. comm.) |
| Lake trout, *Salvelinus namaycush* | Pro, Hpr, Ala, Arg | 1.0 | Hara (pers. comm.) |
| Puffer, *Fugu pardalis* | Pro, Ala, Gly, Bet | 10.0 | Kiyohara *et al.* (1975) |
| Yellowtail, *Seriola quinqueradiata* | Pro, Bet, Try, Val, Ala | 10.0 | Hidaka *et al.* (1985) |
| Amberjack, *Seriola dumerili* | Pro, Try, Bet, Ala | 10.0 | Ishida and Hidaka (1987) |

*Adapted from Hara and Zielinski (1989).
†Abbreviations: AGPA, L-α-amino-β-guanidino propionic acid; L-Ala, L-alanine; Arg, arginine; Asn, L-asparagine; Asp, L-aspartic acid; Bet, betaine; CysH, L-cysteine; Glu, L-glutamic acid; Gly, glycine; Hpr, hydroxy-L-proline; Leu, L-leucine; Met, methionine; Phe, L-phenylalanine; Pro, L-proline; Ser, L-serine; Try, L-tryptophan; Val, valine.
‡Formerly *Salmo gairdneri*.
*Note:* amino acids are listed in the order of relative effectiveness based solely on the mean magnitude of the integrated taste response to each stimulus.

highly effective stimuli, which suggests that similar amino acids may provide important cues for both food searching and ingestive behaviour in the channel catfish. The difference in sensitivity of oral and extra-oral taste buds appears to reflect the difference in the functions of the two (cranial nerves VII v. IX, X) taste systems in catfishes. The extraoral, facial taste system is important in food-searching behaviour and in the picking up of potential food material, while the glossopharyngeal/vagal, oral taste system is primarily involved in the final acceptance or rejection of these substances. Thus, in food search, high sensitivity of facially innervated taste buds is more beneficial to the organism than in the final decision over whether to accept or reject material already present in relatively high concentration within the oropharyngeal cavity. Accordingly, recent investigations have indicated different patterns of central neuronal connectivity for each system, suggesting differential processing of the gustatory inputs to the central nervous system (Finger and Morita, 1985; Morita and Finger, 1985; Kanwal and Finger, Chapter 5 herein). The only other work to have contrasted the sensitivities and specificities of taste buds innervated by different cranial nerves was performed by Sutterlin and Sutterlin (1970), who showed some differences in taste sensitivity to salts, acid and sugars from recordings from the facial and glossopharyngeal nerves in the Atlantic salmon, *Salmo salar*. Interestingly, there was an inverse relationship in the rank order of stimulatory effectiveness for the salts tested between the facial and glossopharyngeal nerves. No other reports exist for comparisons of taste responses across the different cranial nerves.

Most electrophysiological studies of fish taste responses to amino acids are based on whole nerve or nerve twig recordings, where the peak height of the integrated response of the multiunit activity is the measured response parameter. These electrophysiological recordings suggest that the gustatory response to amino acids is highly species specific (Table 9.1); in contrast, the olfactory response spectra to amino acids are relatively similar among the fishes tested (Hara, 1975; Goh *et al.*, 1979; Caprio, 1984; Hara, Chapter 8 herein). Although different species of teleosts may have very different rank orders of effective taste stimuli, certain amino acids, such as L-alanine and L-proline, appear to be effective across the species studied (Table 9.1).

The dose–response (D–R) relationships for amino acids are described in the literature as power functions (channel catfish, Caprio, 1975; topmouth minnow, *Pseudorasbora parva*, Kiyohara *et al.*, 1981), logarithmic functions (Japanese eel, *Anguilla japonica*, Yoshii *et al.*, 1979; red sea bream, *Chrysophrys major*, Goh and Tamura, 1980a) or sigmoidal functions (common carp, *Cyprinus carpio* L., and rainbow trout, *Oncorhynchus mykiss*, Marui *et al.*, 1983a,b). With increasing suprathreshold concentrations of a stimulus, the magnitude of the response will generally increase until saturation of the receptors occurs or the solubility limit of the stimulus is achieved. In some species the D–R functions for different amino acids are different (Marui *et al.*, 1983b). Also, the choice of a particular mathematical function is due primarily to the range of stimulus concentrations the experimenter chooses for the function to best fit the experimental data (Caprio, 1984). For example, power and logarithmic functions do not truncate, but extend infinitely, which is certainly different from biological processes, such as the binding of chemical stimuli to chemoreceptor molecules. Thus, some D–R relations appear to fit a power function relationship over the range of the dynamic response, but because of response saturation occurring at high stimulus concentrations, a sigmoidal relationship is presented (Marui *et al.*, 1983a,b). Also critical in the determination of the best fit function to represent the D–R relation is the duration of the interstimulus interval (ISI) between successive increases in stimulus concentration. As the concentration is raised, longer ISIs are required to allow for the maximal response of the system, owing to increasing effects of sensory adaptation. Thus, different mathematical relationships between dose and response may be obtained dependent solely upon the experimental ISI. Therefore, because of these variables, it is often difficult directly to compare stated D–R relations across species in an attempt to glean possible differences in mechanisms.



Electrophysiological thresholds determined from facial nerve recordings for the more stimulatory amino acids in the majority of the species of teleosts studied generally ranged between $10^{-6}$ M and $10^{-9}$ M (Caprio, 1984). Although there appear to be major sensitivity differences for amino acids between certain teleost species, such as the channel catfish (Caprio, 1978) and the puffer (Hidaka *et al.*, 1976), some of the minor differences reported in taste thresholds may in part be due to the solvent and perfusate used by the different laboratories, e.g. distilled water, artificial pond or natural (tap) water, or artificial or natural seawater. Differences in background levels of amino acids in these waters would have profound effects on the experimentally determined thresholds.

## 9.3 RESPONSE FEATURES FOR SIMPLE CHEMICAL COMPOUNDS

### Amino acids

The results of investigations concerning amino acid taste in teleosts indicate that taste receptor molecules have rather rigid requirements for the molecular structure of the stimulus molecules (Bryant *et al.*, 1989; Bryant and Leftheris, 1991; Marui *et al.*, 1983a,b; Wegert and Caprio, 1991). This indicates that taste receptors require specific conformations of stimuli to bind and activate the transduction process(es) within the taste receptor cell. For example, gustatory responses to amino acids in teleosts are highly stereospecific (Caprio, 1978; Yoshii *et al.*, 1979; Kiyohara *et al.*, 1981; Marui *et al.*, 1983a,b, 1986; Marui and Kiyohara, 1987). The L-isomer of an amino acid has for most species of teleosts studied been shown to be more

stimulatory than its D-enantiomer (Caprio, 1978; Yoshii *et al.*, 1979; Kiyohara *et al.*, 1981; Marui *et al.*, 1983a,b, 1986; Marui and Kiyohara, 1987). However, recently reported data on the facial taste system of the sea catfish, *Arius felis*, revealed a group of taste fibres that were more responsive to D-alanine (Michel and Caprio, 1991; Section 9.5). It remains to be determined whether D>L amino acid sensitivity is more commonplace among marine than freshwater teleosts, or whether the taste system of the D-alanine fibre type of *Arius* is just peculiar to that species. Nevertheless, whether L- or D-amino acids are more stimulatory than their enantiomers, stereospecificity of the taste responses to amino acids is the general rule.

Unsubstituted, L-alpha amino acids are primarily the more stimulatory compounds to the taste systems of teleosts. The primary exceptions are: (1) betaine (N-trimethyl-glycine) is highly stimulatory to a number of marine (Ishida and Hidaka, 1987), but not freshwater, teleosts; (2) both alpha- and beta-alanine are equally stimulatory to palatal taste buds in the Japanese eel, *Anguilla japonica* (Yoshii *et al.*, 1979), and (3) primary carboxyl esters of some amino acids may be (a) similarly stimulatory (Caprio, 1978), or (b) more stimulatory (Kiyohara *et al.*, 1981), or (c) less stimulatory (Yoshii *et al.*, 1979; Marui *et al.*, 1983a; Bryant *et al.*, 1989; Bryant and Leftheris, 1991), or (d) either more or less stimulatory, depending upon the specific ester (Marui *et al.*, 1983b), than the parent free amino acid. However, a recent report (Bryant and Leftheris, 1991) suggested that the high level of gustatory neural activity in response to esters of L-alanine in the channel catfish (Caprio, 1978) was likely due to stimulation by free L-alanine which was released by alkaline hydrolysis of the esters. Unsubstituted, L-alpha amino acids are also more stimulatory than simple peptides. The rule that was established for the taste system of the channel catfish (Caprio, 1978), and for which no exceptions have yet been shown for any species of teleost tested (Kiyohara *et al.*, 1981; Hidaka and Ishida, 1985; Marui and Kiyohara, 1987), is that a peptide is less effective than its most stimulatory amino acid residue; furthermore, the order of the amino acid residues in a simple peptide does not significantly affect its ability to stimulate the taste system (Caprio, 1978; Hidaka and Ishida, 1985; Marui and Kiyohara, 1987).

As indicated by Hara and Zielinski (1989), among the teleosts whose taste responses were examined systematically, two general groups were identified: (1) those whose facial taste systems respond to many different types of amino acids (i.e. 'wide response range' in Table 9.1), with varying stimulatory effectiveness depending upon the particular amino acid tested, and (2) those whose facial taste systems are highly selective and respond to few of the amino acids tested (i.e. 'limited response range'). So far, of 19 species whose facial taste systems have been tested with amino acids, 9 species consisting of both freshwater and marine organisms are indicated to be of the limited response range (Table 9.1). In general, regardless of whether fish had taste systems with wide or limited response ranges, neutral amino acids



containing two or fewer carbon atoms having unbranched and uncharged side chains and the imino acid, L-proline, were highly stimulatory. With few exceptions, acidic amino acids were poor gustatory stimuli. Taste responses to the basic amino acids, generally L-arginine, were quite variable depending upon the species. In the channel catfish (Caprio, 1975), the Japanese eel (Yoshii *et al.*, 1979), the red sea bream, and mullet, *Mugil cephalus* (Goh and Tamura, 1980a), the topmouth minnow (Kiyohara *et al.*, 1981), the maaji jack mackerel, *Trachurus japonicus* (Ishida and Hidaka, 1987), and an African cichlid, *Tilapia nilotica* (Marui, unpublished), at least one of the basic amino acids was highly effective. In other species, such as the common carp (Marui *et al.*, 1983a), the rainbow trout (Marui *et al.*, 1983b), the brook charr, *Salvelinus fontinalis* (Hara, unpublished), the aigo rabbitfish, *Siganus fuscescens* (Ishida and Hidaka, 1987) and the isaki grunt, *Parapristipoma trilineatum* (Ishida and Hidaka, 1987), the basic amino acids were non-stimulatory or resulted in minimal taste activity. It was reported (Marui *et al.*, 1983b), however, for the rainbow trout that L-arginine and its derivatives became quite active at basic pH (> 8.5). It is most probable that the differences in amino acid specificity noted above for the different teleosts is related to the particular feeding niche of the respective species.

### Aliphatic acids

Aliphatic acids have also been shown to be stimulatory to the taste system of the Japanese eel (Yoshii *et al.*, 1979), the Atlantic salmon (Sutterlin and Sutterlin, 1970) and the common carp (Marui, unpublished; Table 9.2). The magnitude of the integrated taste response of the eel is greater for carboxylic acids than for amino acids at 1 mM. The gustatory threshold for carboxylic acids on the palatine taste buds of the eel ranged between 100 nM and 0.1 mM, and the D–R curves for some carboxylic acids were steeper than for the corresponding amino acids. Treatment of the taste epithelium of the eel with papain (a protease used to inactivate membrane bound taste receptor proteins) caused taste responses to three of four amino acids tested to be eliminated, but this treatment had little effect on taste activity to acetic acid. Also, there was little cross-adaptation between amino acids and carboxylic acids having the same carbon chain length. These last two results suggested that carboxylic acids stimulate receptors independent from those that bind amino acids.

The magnitude of the taste responses of the Atlantic salmon and Japanese eel generally increased with increasing carbon chain length of the aliphatic acid. In the carp, both aliphatic and aromatic carboxylic acids stimulated the facial taste system (Table 9.2). Although compounds consisting of two carbon atoms were more stimulatory than those containing one carbon atom for both groups of acids, the taste responses to the monocarboxylic acids peaked at compounds containing between three and five carbons,

Table 9.2 Relative stimulatory effectiveness of carboxylic acids tested at 1 mM on the taste receptors of carp, *Cyprinus carpio*, as a percentage of the response to the standard, 1 mM L-alanine

| *Chemicals** | *Structural formula* | *Stimulatory effectiveness (%) (mean ± SD)* | *Number of tests* |
|---|---|---|---|
| *Aliphatic carboxylic acid* | | | |
| Monocarboxylic acid | | | |
| Formic acid | HCOOH | 22.5 ± 12.2 | 5 |
| Acetic acid | $CH_3COOH$ | 97.4 ± 24.4 | 7 |
| Propionic acid | $CH_3CH_2COOH$ | 128.0 ± 18.7 | 7 |
| n-Butyric acid | $CH_3(CH_2)_2COOH$ | 113.8 ± 18.9 | 4 |
| n-Valeric acid | $CH_3(CH_2)_3COOH$ | 135.6 ± 9.8 | 5 |
| Caproic acid | $CH_3(CH_2)_4COOH$ | 99.8 ± 41.7 | 4 |
| Dicarboxylic acid | | | |
| Oxalic acid | HOOCCOOH | 0 | 3 |
| Malonic acid | $HOOCCH_2COOH$ | 93.2 ± 46.4 | 2 |
| Succinic acid | $HOOC(CH_2)_2COOH$ | 259.2 ± 40.8 | 2 |
| Glutaric acid | $HOOC(CH_2)_3COOH$ | 350.6 ± 86.9 | 2 |
| Adipic acid | $HOOC(CH_2)_4COOH$ | 308.5 ± 54.0 | 2 |
| Pimelic acid | $HOOC(CH_2)_5COOH$ | 128.4 ± 46.0 | 2 |
| Tartaric acid | HOOCCHOHCHOHCOOH | 59.0 ± 28.2 | 6 |
| Tricarboxylic acid | | | |
| Citric acid | $HOOCCH_2C(OH)(COOH)CH_2COOH$ | 245.1 ± 72.6 | 4 |
| *Aromatic carboxylic acid* | | | |
| Benzoic acid | $C_6H_5COOH$ | 32.5 ± 7.8 | 2 |
| Salicylic acid | $HOC_6H_4COOH$ | 5.0 ± 7.0 | 2 |
| Phthalic acid | $C_6H_4(COOH)_2$ | 25.0 ± 2.8 | 2 |

*All chemicals were adjusted in neutral range (pH 6.8–7.1): see text for explanation.



whereas for dicarboxylic acids, taste responses were maximal for compounds containing five to six carbon atoms. It is important to note that all stimuli in Table 9.2 were pH adjusted with 0.1 N sodium hydroxide and that 1 mM sodium chloride was not an effective taste stimulus in the carp (Marui *et al.*, 1983a); therefore, the taste activity recorded in response to the compounds listed was due primarily to the carboxylic anions rather than to the sodium ion.

### Nucleotides

Kiyohara *et al.* (1975) first indicated that nucleotides might be important gustatory stimuli to teleosts. Nucleotides, such as adenosine-5′-monophosphate (AMP), inosine-5′-monophosphate (IMP), uridine-5′-monophosphate (UMP), and adenosine-5′-diphosphate (ADP), were stimulatory to the lip taste buds of the puffer, *Fugu pardalis*. Single fibre analyses revealed that facial taste fibres in the puffer were divided into three groups: (1) those responding well to hydrochloric acid, (2) those responding well to nucleotides, and (3) those responding well to amino acids. Also, a preliminary study in the channel catfish (Michel *et al.*, 1987) implied that nucleotide taste information is transmitted to the central nervous system by fibres that are not especially sensitive to amino acids. Since the work on the puffer, nucleotides have been found to be excitatory gustatory stimulants for the following species of teleosts: oriental weatherfish, *Misgurnus anguillicaudatus* (Harada, 1986); yellowtail, *Seriola quinqueradiata* (Harada, 1986; Hidaka *et al.*, 1985); amberjack, *Seriola dumerili* (Ishida and Hidaka, 1987); jack mackerel, *Trachurus japonicus* and club mackerel, *Scomber japonicus* (Ishida and Hidaka, 1987); rabbit fish, *Siganus fuscescens* (Ishida and Hidaka, 1987); tiger fish, *Therapon oxyrhynchus* (Hidaka and Ishida, 1985); grunt, *Parapristipoma trilineatum* (Ishida and Hidaka, 1987); carp (Marui, unpublished), and channel catfish (Littleton *et al.*, 1989). The ability to detect nucleotides is not limited to the taste system of fishes, but has also been found for the olfactory system of the channel catfish (Michel *et al.*, 1987) and for gustatory and olfactory systems of crustaceans, such as shrimp, *Palaemonetes pugio* (Carr and Thompson, 1983; Carr and Derby, 1986a,b), lobster, *Homarus americanus* (Derby and Atema, 1982a,b), crayfish, *Austropotamobius torrentium* (Hatt, 1984) and spiny lobster, *Panulirus argus* (Derby *et al.*, 1984; Carr *et al.*, 1986). Interestingly, the threshold range for nucleotides in the taste system of teleosts (10–100 μM) is similar to that reported for the rat (Yoshii *et al.*, 1986), and is significantly higher than that determined for amino acids in the facial taste systems of fishes.

### Bile salts

The detection of bile salts, which are potent gustatory and olfactory stimuli to salmonids, is proposed to be important in homing migration (Döving *et al.*,

1980; Selset and Döving, 1980). These compounds, however, are quite different from other gustatory stimuli, such as amino acids, aliphatic acids and nucleotides, in that bile salts have been shown to stimulate the facial taste system of only salmonids (Hara *et al.*, 1984). Unpublished data (Marui) indicate that the taste systems neither of the common carp, nor of the sea catfish, *Plotosus lineatus*, nor of an African cichlid, *Tilapia nilotica*, are stimulated by up to 0.1 mM bile salts. Integrated taste responses recorded from the palatine nerve in the rainbow trout to taurolithocholate, the most effective bile salt tested, increased linearly with logarithmic increase in concentration (Hara *et al.*, 1984). The threshold ranged between 1 and 10 pM, which is approximately four log units lower than that for L-proline, the most potent amino acid taste stimulant for that species (Marui *et al.*, 1983b). Taurodeoxycholic and cholic acids, less effective stimuli than taurolithocholic acid, were nevertheless far more potent taste stimuli than L-proline. The functional significance for taste systems of salmonids to be sensitive to bile salts is unknown; possibly, both olfaction and taste are involved in the detection of key stimulus compounds that are involved in homing behaviour.

## 9.4 RECEPTOR SITE TYPES FOR AMINO ACIDS

Although studies published since 1975 established conclusively that the taste system of teleosts detects amino acids with high sensitivity, little was known concerning the types (defined by their specificities) of amino acid taste receptor sites that exist on the taste cells. Information on receptor site types for amino acids in teleosts has primarily been obtained from electrophysiological cross-adaptation and biochemical competitive binding experiments performed primarily in the channel catfish. Both the electrophysiological and biochemical experiments indicated the existence of a multiplicity of relatively independent amino acid receptor site types; further, the electrophysiological studies indicated that the types and specificities of these receptor sites varied across species (Table 9.3; Brand and Bruch, Chapter 7 herein).

Two different electrophysiological cross-adaptation paradigms were used for determining the types of amino acid receptors that exist for the species listed in Table 9.3. In the first method, the 'test' stimulus is presented just after the response to a single presentation of the 'adapting stimulus' has returned to baseline (for the eel and puffer); in the second scheme, the 'test' stimulus is injected into an 'adapting stimulus' that continuously bathes the sensory epithelium (for the carp, channel catfish and rainbow trout). Test amino acids whose responses were suppressed completely (to control levels) by the adapting stimulus are presumed to share a common receptive pathway and possibly the same receptor site. Those test amino acids that remain stimulatory are considered to have at least some portion of their



Table 9.3 Classification of receptor types by cross-adaptation experiments

| *Species** | *Receptor types*† |
|---|---|
| Carp[1] | (1) L-Ala (L-Pro, L-Ser, Gly, L-α-Abu, β-Ala) |
| | (2) L-CysH |
| | (3) L-His |
| | (4) L-Glu |
| | (5) L-Asp |
| | (6) Bet |
| Japanese eel[2] | (1) L-Ala (L-Lys, L-Arg, L-Ser, Gly) |
| | (2) L-Pro |
| | (3) L-His |
| | (4) Bet |
| Channel catfish[3] | (1) L-Ala (Gly, L-Ser, L-Met) |
| | (2) L-Arg |
| | (3) L-Pro |
| | (4) L-Lys |
| | (5) L-His |
| | (6) D-Ala[3,4] |
| | (7) D-Arg |
| | (8) D-Pro |
| Rainbow trout[5] | (1) L-Pro |
| | (2) L-Leu |
| | (3) L-AGPA (Bet) |
| Puffer[6] | (1) L-Ala (Gly, L-Ser, Sarcosine) |
| | (2) L-Pro (Trimethylglycine) |
| | (3) Bet (Dimethylglycine) |

*Sources: 1, Marui *et al.* (1987); 2, Yoshii *et al.* (1979); 3, Caprio, (1982), Wegert and Caprio (1991); 4, Brand *et al.* (1987); 5, Hara and Marui (1982); 6, Kiyohara *et al.* (1991).

†Chemicals set in bold enhance the responses to amino acids. Abbreviations: Abu, alpha-aminobutyric acid; AGPA, alpha-amino-beta-guanidino-propionic acid; Ala, alanine; Arg, arginine; Asp, aspartic acid; Bet, betaine (N-trimethyl-glycine); CysH, cysteine; Glu, glutamic acid; Gly, glycine; His, histidine; Hpr, hydroxyproline; Hyp, hydroxyproline; Leu, leucine; Lys, lysine; Met, methionine; Phe, phenylalanine; Pro, proline; Sarcosine, N-methyl glycine; Ser, serine; Try, tryptophan; Val, valine.

Note: the compounds included with a parenthesis are thought to bind to the same receptor sites as the initially listed amino acid in each row.

receptive pathways (and therefore receptor sites) independent from that of the adapting stimulus.

It is important to note, however, that in addition to differences in how the adapting stimulus was presented as noted above, an additional difference in the testing paradigm still remains and may be a factor in the results obtained. The concentrations of the adapting and test stimuli vary across the species tested. For the majority of the experiments, the stimuli were tested at a single concentration, usually $10^{-4}$ M or $10^{-3}$ M. For the

channel catfish (Wegert and Caprio, 1991), however, all stimuli for each fish tested were adjusted in concentration to be equipotent stimuli. This concentration adjustment allows each stimulus, independent of its relative stimulatory effictiveness, to have equal effect in eliciting a similar magnitude of action potential activity along the gustatory neurones. For relatively independent receptor sites, this also allows a poor agonist, because of its higher concentration, to have a chance of competing for the receptor site approximately equal to that of a more stimulatory agonist at lower concentration. Using this testing paradigm, eight different receptor site types for amino acids were indicated in the facial taste system of the channel catfish (Wegert and Caprio, 1991) (Table 9.3). Based on the magnitude of the taste responses to the eight different amino acid stimuli, the binding sites for L-alanine, L-arginine and L-proline appear to be in relatively large numbers. Recently, experiments utilizing membrane vesicles isolated from the cutaneous taste epithelium of the channel catfish that were incorporated into phospholipid bilayers on the tips of patch pipettes (see Chapter 7), have confirmed the existence of both the arginine (Teeter *et al.*, 1990) and proline (Kumazawa *et al.*, 1990) receptor sites. These and other recent advances concerning receptor site identification and the biochemical processes of transduction in the taste system of the channel catfish are summarized by Brand and Bruch (Chapter 7 herein).

There are few generalities concerning receptor site types for amino acids in teleosts that can be summarized from the limited number of species tested electrophysiologically (Table 9.3). Other than the indication of multiple receptor site types for amino acids in the same species, there is an indication in the carp (Marui *et al.*, 1987), Japanese eel (Yoshii *et al.*, 1979), channel catfish (Wegert and Caprio, 1991) and puffer (Yamashita *et al.*, 1987) that some of the neutral amino acids may share the same or highly cross-reactive receptive pathways. In contrast, the receptor sites for the basic amino acids may be different from that (or those) indicated for the neutral amino acids, in that the L-isomers of arginine, lysine and histidine in the channel catfish were all indicated to have relatively independent receptor sites (Wegert and Caprio, 1991). A similar finding occurred in the carp for the acidic amino acids, where the facial taste receptor sites for the L-isomers of aspartic and glutamic acids were indicated to be relatively independent (Marui *et al.*, 1987). Also, from data obtained from the channel catfish, it is evident that receptor sites for the stereoisomers of particular amino acids may be different (Brand *et al.*, 1987; Wegert and Caprio, 1991). Evidence from four of the five species listed in Table 9.3 also indicated that betaine binds to receptor sites independent from those to other amino acids. However, from unpublished experiments in the sea catfish, *Plotosus lineatus* (Caprio, Marui and Kiyohara), L-proline and betaine bind to the same receptor site with similar affinities.



## 9.5 TASTE RESPONSES OF SINGLE FACIAL TASTE FIBRES

Although much is known concerning multiunit taste responses of certain species of teleosts to amino acids, quantitative studies of the responses of single facial taste fibres to these stimuli are rare. A major question related to quality coding of amino acid taste information is how that information is represented in the output of single peripheral taste neurones. A knowledge of the 'tuning' (i.e. response specificity) of individual neurones to amino acid stimuli is critical to a better understanding of how the organism may identify the stimulus.

The first quantitative study of single fibre taste activity in a teleost to amino acid stimuli was performed in the Japanese puffer, *Fugu pardalis* (Kiyohara *et al.*, 1975). That study indicated that amino acids, nucleotides and hydrochloric acid activated different facial taste fibres, although betaine stimulated both the amino acid and hydrochloric acid fibres. Another study of the responses of individual facial taste fibres in the puffer reported that only 16 of the 106 fibres isolated responded to L-proline, the only amino acid tested. The remaining fibres responded to nucleotides, hydrochloric acid or mechanical stimulation (Kiyohara *et al.*, 1985). Two more recent reports on the puffer indicated that although L-alanine and L-proline activate different receptor sites (based on electrophysiological, cross-adaptation data) (Kiyohara *et al.*, 1989), these stimuli excite the same taste fibres (Marui and Kiyohara, 1987).

The responses of individual facial taste fibres to amino acids were also reported in the North American, freshwater channel catfish, *Ictalurus punctatus* (Davenport and Caprio, 1982). Since the facial taste system of the channel catfish responded to all the common amino acids (Caprio, 1975, 1978, 1982), it was of interest to determine whether the amino acid receptor sites and taste cells were organized in such a manner to allow for the existence of different fibre types. Nine of 15 single recurrent facial taste fibres that innervated taste cells on the flank of the animal were stimulated best by L-alanine, whereas the remaining six fibres were stimulated best by L-arginine. A more recent quantitative study indicated that of the 94 facial taste fibres analysed that innervated maxillary barbel taste buds in *I. punctatus* 49 were L-alanine-best and 42 were L-arginine-best taste fibres (Kohbara and Caprio, unpublished). The responses from each of the two fibre groups clearly showed that the L-arginine fibre type was narrowly tuned; one portion of the arginine-best fibres responded with high frequency to only L-arginine, whereas the remaining portion responded well both to L-arginine and to L-proline. The L-alanine fibre type was responsive primarily to a number of neutral amino acids. It is rather interesting that transduction of L-alanine taste information, transmitted primarily by the L-alanine neural channel (i.e. fibre type) to the facial lobe of the medulla (the primary gustatory centre), probably involves G-proteins and second-messenger

systems (Bruch and Kalinoski, 1987, 1988), whereas the transduction of arginine (Teeter *et al.*, 1990) and proline (Kumazawa *et al.*, 1990) information, transmitted by the L-arginine neural channel, is thought to occur through direct ligand-operated ion channels (see also Brand and Bruch, Chapter 7 herein). Thus, not only were the taste receptor sites for the L-isomers of alanine, arginine and proline relatively independent from one another in the taste system of *Ictalurus* (Section 9.4), but there was a differential innervation of these taste cells by the two major types of facial taste fibres. In addition, a small number of D-alanine-best fibres was indicated from recordings from small twigs of the facial nerve in the channel catfish (Wegert and Caprio, 1991). Also, as found for the puffer, nucleotide-sensitive fibres are different from the major amino-acid-sensitive, facial taste fibres in *Ictalurus* (Kohbara, Michel and Caprio, unpublished).

An analysis of responses from single facial taste fibres in the North American sea catfish, *Arius felis*, also indicated the presence of two major types of amino-acid-sensitive fibres (Michel and Caprio, 1991). Similar to that found in *Ictalurus*, the major fibre type present in *Arius* (22 of 42 fibres analysed) was highly sensitive to L-alanine. However, glycine, which in *Arius* was approximately equally stimulatory to L-alanine, was much less stimulatory to the taste system of *Ictalurus*. In addition, the sensitivity of the *Arius* facial taste system to L-arginine was much lower than that indicated for *Ictalurus*, and the second most common fibre type in *Arius* was most responsive to D-alanine. For these D-alanine units, L-alanine was the second most effective amino acid, whereas in general the L-alanine/glycine units responded poorly to glycine. Thus, it appears that the detection of D-alanine and possibly other D-isomers might be important to the feeding behaviour of *Arius*. These findings are reasonable in that D-alanine was recently shown to be in measurable levels in 18 of 43 invertebrate species tested, and that D-amino acids were more abundant than their L-isomers in six species of bivalve molluscs (Preston, 1987; Felbeck and Wiley, 1987).

The major amino-acid-sensitive, facial taste fibres of the Indo–Pacific sea catfish, *Plotosus lineatus*, also consisted of two types of fibres, those that were most stimulated by L-proline and betaine, and those that were most stimulated by L-alanine and glycine (Caprio, Marui and Kiyohara, unpublished). Thus, the input of amino acid taste information to the central nervous system (i.e. the facial lobe of the medulla) in *I. punctatus*, *A. felis* and *P. lineatus*, each species being a member of a different family of catfishes, occurs primarily through only two major types of neural channel (i.e. fibre types). Whether this will be similar for other species of catfish and non-siluriform teleostean species, and how this organization is used by the organism to determine stimulus quality, are unknown. Additional studies of the response specificity of individual taste fibres (facial, glossopharyngeal and vagal) in other teleostean species are necessary for a better understanding of the organization of amino acid neural channels in teleosts.



## 9.6 ENHANCED TASTE ACTIVITY

Chemoreceptors in nature rarely, if ever, are presented with single pure stimuli. As a rule, chemical stimuli in nature are rather complex mixtures, and the peripheral taste and olfactory systems must be organized to detect and process this information centrally. As such, animal extracts and certain mixtures of amino acids were shown to be potent stimuli to fishes (Konosu *et al.*, 1968; Funakoshi *et al.*, 1981; Carr, 1976; Carr and Chaney, 1976; Hidaka *et al.*, 1976, 1978; Adron and Mackie, 1978; Yoshii *et al.*, 1979; Goh and Tamura, 1980a,b; Mackie *et al.*, 1980; Ellingsen and Döving, 1986; Marui and Kiyohara, 1987; Marui *et al.*, 1987; Kiyohara *et al.*, 1989). However, although particular animal extracts or mixtures of amino acids were shown to be stimulatory, individual components of some of these mixtures were shown to be inactive or weak stimulants. So, it is suggested that the stimulatory ability of certain mixtures is due to potentiation or synergistic interactions among the components.

In electrophysiological experiments, synergistic effects were observed qualitatively for mixtures of betaine and amino acids in the taste systems of several species of fish (Hidaka *et al.*, 1976; Yoshii *et al.*, 1979). A betaine and L-alanine mixture resulted in enhancement of taste activity in the puffer (Hidaka *et al.*, 1976). Also in the same species, single unit responses to alanine and glycine were potentiated by the presence of betaine in cross-adaptation experiments (Marui and Kiyohara, 1987; Kiyohara *et al.*, 1989). Mixtures of particular amino acids and betaine also enhanced feeding behaviour in some fishes (Hidaka *et al.*, 1978; Goh and Tamura, 1980b; Mackie *et al.*, 1980). In a quantitative electrophysiological study of the effects of amino acid cross-adaptation in the carp, an enhancement of gustatory responses to amino acids with betaine and with L-aspartate-Na was clearly shown (Marui *et al.*, 1987); however, the enhancement observed for some pairs of stimuli might be fibre specific because the variability in the multiunit taste responses recorded was considerable. In the facial taste system of the carp, cross-adaptation with 1 mM betaine resulted in a shift in the D–R function for L-alanine to a lower concentration range (about 4 log units), whereas betaine alone at stimulus concentrations between $10^{-8}$ and $10^{-13}$ M was ineffective (Marui *et al.*, 1987). Conversely, the D–R function for betaine during adaptation with 1 mM L-alanine was also shifted to a lower concentration range. Although synergism was observed in the taste system of the Japanese eel in response to binary mixtures of betaine with an amino acid, this same effect was also observed with other binary amino acid mixtures not containing betaine (Yoshii *et al.*, 1979).

The mechanisms proposed for the taste enhancement that occurs with certain mixtures are varied. It was suggested for the Japanese eel that synergism might be caused by the weakening of the negative cooperativity between specific amino acid receptor sites (Yoshii *et al.*, 1979). Because of a

linear relationship between the integrated taste response and the log stimulus dose over a wide concentration range, it was postulated that this occurred as a result of negative cooperativity between amino acid receptor sites (i.e. it required increasingly large elevations in stimulus concentration to provide the same relative increase in the height of the integrated taste response). Thus, lessening of the negative cooperativity between sites would result in greater taste activity. Similarly, positive cooperativity between certain sites would also result in enhanced neural activity. A mechanism offered for the synergism observed electrophysiologically between 5'-nucleotides and L-amino acids in taste responses in the rat was an increase in affinity of the stimulus for the receptor site (Yoshii *et al.*, 1986); however, biochemical evidence suggested that an increased number of available binding sites, and not an increased affinity for the ligands, was responsible for the enhanced taste activity (Torii and Cagan, 1980; Cagan, 1987).

Enhancement of olfactory (Caprio *et al.*, 1989; Kang and Caprio, 1991) and gustatory (Kohbara and Caprio, unpublished) neural activity in catfish to particular mixtures of amino acids, presented simultaneously rather than sequentially, as in the previously described cross-adaptation experiments, has also been documented. Here, the mechanism suggested for the resulting enhanced neural activity is the simultaneous activation of multiple receptor site types by the components in the mixtures.

## 9.7 BEHAVIOUR TO CHEMICAL STIMULI

A number of studies have shown conclusively that amino acids acting singly and in combination stimulate feeding behaviour in fishes (Hashimoto *et al.*, 1968; Carr, 1982; Hidaka, 1982; Mackie, 1982; Sutterlin *et al.*, 1982; Little, 1983; Takeda *et al.*, 1984; Harada, 1985; Mearns, 1985, 1986; Olsén *et al.*, 1986; Jones, 1989 and Chapter 14 herein). Although given the extreme paucity of chemosensory information concerning all but a few species of teleosts, a correlation between the potent amino acids determined electrophysiologically and those determined behaviourally is indicated for the channel catfish, Japanese eel, red sea bream and puffer (Table 9.4). In the red sea bream, a correlation of 0.78 was found between the amino acids that were effective in initiating feeding behaviour and those that stimulated gustatory neural activity, whereas a correlation of only 0.01 occurred between the behaviourally effective amino acids and those that were potent olfactory stimuli determined electrophysiologically (Goh and Tamura, 1980a,b). In the puffer, the amino acids that stimulated lip taste buds electrophysiologically were also effective in stimulating feeding behaviour, but the concentration of the amino acids necessary to release the behaviour was greater by 2–3 orders of magnitude than that required to elicit gustatory neural activity (Hidaka *et al.*, 1978). In the channel catfish, taste thresholds for the more stimulatory amino acids tested electrophysiologically



Table 9.4 Potent amino acids determined by electrophysiology and behaviour

| *Species* | *Electrophysiology*†* | *Feeding behaviour*†* |
|---|---|---|
| Channel catfish, *Ictalurus punctatus* | L-Ala, L-Arg, L-Pro[1,2] | L-CysH[3], L-Arg, L-Met[4], L-Ala, L-Arg, L-Pro[5] |
| Japanese eel, *Anguilla japonica* | L-Arg, Gly, L-Ala, L-Pro[6] | L-Arg, L-Ala, Gly[7] |
| Puffer, *Fugu pardalis* | Gly, L-Pro, Bet, L-Ala[8] | L-Pro, Bet, L-Ala, Gly[9] |
| Rainbow trout, *Oncorhynchus mykiss* | L-Pro, L-Hyp, L-Leu, L-Ala[10] | (L-Tyr, L-Phe and L-His) or (L-Tyr, L-Phe and L-Lys)[11] |
| Red sea bream, *Chrysophrys major* | L-Ala, Gly, L-Arg, L-Ser[12] | L-Ala, Gly, L-Ser[13] |

*Sources: 1. Caprio (1975); 2. Kanwal and Caprio (1983); 3. Little (1977); 4. Holland and Teeter. (1981); 5. Valentincic and Caprio (unpublished); 6. Yoshii *et al.* (1979); 7. Hashimoto *et al.* (1968); 8. Hidaka *et al.* (1976); 9. Hidaka *et al.* (1978); 10. Marui *et al.* (1983b); 11. Adron and Mackie (1978); 12. Goh and Tamura (1980a); 13. Goh and Tamura (1980b).
†Abbreviations as in Table 9.3.

(Caprio, 1978; Davenport and Caprio, 1982) and behaviourally (Holland and Teeter, 1981; Valentincic and Caprio, unpublished) were reported to be in fair agreement.

A comparison of the results obtained electrophysiologically (Marui *et al.*, 1983b) and behaviourally (Adron and Mackie, 1978) in the rainbow trout, however, is confusing. The L-isomers of tyrosine, phenylalanine and either lysine or histidine were the constituents of the simplest mixture tested that stimulated feeding activity. When this mixture was subdivided into two fractions, neither fraction was active. When these same compounds were omitted from the effective mixture (i.e. the mixture which applied to casein food pellets caused a significantly greater number of daily actuations of the food dispenser trigger than did the unflavoured casein pellets) of L-amino acids constituting an artificial squid extract, the resulting mixture was not reduced in its stimulatory ability. Amazingly, lysine, tyrosine and histidine were inactive taste stimuli determined electrophysiologically (Marui *et al.*, 1983b). Of the four amino acids identified above, electrophysiological studies indicated histidine and phenylalanine to be an effective olfactory (Hara, 1973) and gustatory (Marui *et al.*, 1983b) stimulus, respectively. In addition, proline, which was in highest concentration in the synthetic squid extract, was inactive as a feeding stimulus (Adron and Mackie, 1978), but was a potent taste stimulus determined electrophysiologically (Marui *et al.*, 1983b).

Nucleotides and nucleosides are also recognized as effective chemicals in the feeding behaviour of teleosts. In the turbot, *Scophthalmus maximus*, inosine and a few closely related purine nucleotides and nucleosides at low concentrations were specific feeding stimulants (Mackie and Adron, 1978). A weak activity of 5′-IMP and 5′-UMP, and a rather high activity of 5′-GMP were observed in the Japanese eel, although a repellent activity of 5′-AMP was recognized (Takeda *et al.*, 1984). Adult oriental weatherfish and juvenile yellowtail were also stimulated behaviourally by nucleotides (Harada, 1986). In contrast, although nucleotides were shown to be effective physiological taste stimuli in the puffer (Hidaka *et al.*, 1977), these compounds did not evoke feeding behaviour in that species (Hidaka, 1982).

Additional species of teleosts need to be tested both physiologically and behaviourally before a definitive statement can be made concerning the correlation of electrophysiological and behavioural studies of chemoreception. It does appear, however, that in some species there is a stronger relation between the sense of taste and feeding behaviour than that found for olfaction (Goh and Tamura, 1980b). This is consistent with behavioural evidence obtained from bullhead catfish, *Ictalurus nebulosus*, in which the gustatory sense was involved primarily in stimulus localization and swallowing or rejection during feeding (Atema, 1971), whereas the olfactory system served as a general alerting sense involved in social interactions (Todd *et al.*, 1967). Further experiments are required to determine whether this



functional distinction between olfaction and taste indicated for catfish is common among other teleostean species.

## 9.8 TACTILE SENSITIVITY OF PERIPHERAL NEURONES

Mechanosensation and gustation are thought to be intricately involved in food ingestion in fish (Herrick, 1904, 1906; Ariens-Kappers *et al.*, 1960; Bardach *et al.*, 1967; Bartheld and Meyer, 1985). Similarly, in mammals, mechanosensory (trigeminal) information contributes to both the sensorimotor and the motivational control of ingestive behaviour (Zeigler *et al.*, 1984), and the interaction between somatosensation and gustation is involved in palatability (Berridge and Fentress, 1985). The high percentage of bimodal (taste/touch) neurones within the primary gustatory nucleus of the medulla in carp (Marui, 1977) and catfish (Marui and Caprio, 1982; Marui *et al.*, 1988; Hayama and Caprio, 1989) is indicative that somatosensation is at least as important in the feeding processes of fishes as it appears to be for mammals (Kanwal and Finger, Chapter 5 herein).

The possible origins of bimodal (taste and tactile) units in the primary gustatory nucleus of teleosts are numerous. (1) The finding of trigeminal input to the primary gustatory nucleus of the medulla in the puffer (Kiyohara *et al.*, 1985) and the sea catfish (Kiyohara *et al.*, 1986), suggests the possibility of the convergence of mechanically sensitive trigeminal and taste-sensitive facial nerve fibres in the facial lobe (FL). Electrophysiological experiments clearly showed that sectioning the trigeminal and facial nerves, respectively, during microelectrode recordings from bimodal (taste and tactile) FL neurones in the carp resulted in the loss of tactile and taste responses, respectively (Marui and Funakoshi, 1979). (2) The occurrence in the puffer (Kiyohara *et al.*, 1985) and channel catfish (Davenport and Caprio, 1982) of mechanically sensitive facial nerve fibres suggests the possibility of the convergence of mechanically sensitive and taste-sensitive facial fibres, respectively, in the FL. In addition, glossopharyngeal and vagal nerves innervating the oropharyngeal cavity in the channel catfish also contain a large population of mechanosensory fibres (Kanwal and Caprio, 1983). (3) Peripheral nerve fibres responsive to both mechanical and chemical stimulation were also indicated in the channel catfish (Davenport and Caprio, 1982).

## 9.9 SUMMARY

The gustatory sense in the majority of teleosts studied rivals the olfactory sense in terms of sensitivity for particular chemical stimuli. Although a number of different classes of stimuli are known to excite the gustatory receptors of teleosts (e.g. aliphatic acids, bile salts, and nucleotides), research concerning the taste of amino acids has dominated the field since 1975. For

the facial taste system, electrophysiologically determined gustatory thresholds for amino acids are generally reported between micromolar and nanomolar concentrations. Taste buds innervated by glossopharyngeal and vagal nerves appear to have amino acid specificities similar to those of taste buds innervated by facial nerves, but are somewhat less sensitive. Two general types of patterns of taste responses to amino acids occur in teleosts. Some taste systems have a 'wide response range' and detect many of the amino acids, while other species have a 'limited response range' and respond well to only few of the amino acids. Competition experiments indicate that multiple types of amino acid receptors exist within taste receptor cell membranes, and that the organization of these sites is not random, as particular types of taste fibres within the same species have been identified. Generally, L-amino acids are more stimulatory than their stereoisomers, but recent electrophysiological data indicate the existence of D-amino acid taste receptor sites and D-alanine-best facial taste fibres. Certain mixtures of amino acids may result in enhanced (synergistic) taste activity. One mechanism for this enhancement is the simultaneous activation of different receptor site types by the components of the mixture.

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