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Full Papers

Lipid characterization and ^{14}C-acetate metabolism in catfish taste epithelium [1]

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Summary. The catfish, *Ictalurus punctatus* is an important model system for the study of the biochemical mechanisms of taste reception. A detailed lipid analysis of epithelial tissue from the taste organ (barbel) of the catfish has been performed. Polar lipids account for 62 ± 1% of the total, neutrals for 38 ± 1%. Phosphatidyl-cholines, serines and ethanolamines are the major constituents of the polar fraction. Plasmalogen concentration is high relative to that of non-neural tissues. [^{14}C]-Acetate is incorporated into cell lipid fractions after incubation of barbel tissue at 37 °C for 60 min. Percentage amounts of most lipids change with time during this in vitro incubation. The phospholipids are the most metabolically active fractions. This work yields information for continuing reconstitution experiments and indicates that the taste epithelium of this important model system is a metabolically active tissue capable of supporting lipid turnover/synthesis.
Key words. Taste; phospholipid; plasmalogen; ^{14}C-acetate; epithelium.

While the receptor events in taste are beginning to be understood [2, 3], the molecular details of reception and transduction for various qualities are still incompletely described. For example, responsitivity to salt is apparently largely due to the presence in the taste cell membrane of nonvoltage gated (and in most cases, amiloride-sensitive) epithelial channels [4–7]. These channels have yet to be isolated and studied in vitro, and their stability and conformational characteristics are not known. Response to sour (acidic) stimuli may be mediated by a proton block of outward potassium current [8]. There is suggestive evidence for receptor-mediated responses to sweet stimuli [9–11], but molecular details are not known. Receptor mechanisms for bitterness have not been explored in depth [3].

Much of the slow progress in the past in understanding the molecular mechanisms of taste stemmed from the lack of suitable animal models. Recently, however, the amino acid taste system of the catfish has been exploited as a model. The taste system of this animal shows a high degree of sensitivity and specificity for amino acids [13–16]. The barbels of the catfish are especially dense in taste buds particularly on the leading and trailing edge of the barbel (the barbel is elliptical in cross-section) where the sensory nerves traverse the length of the organ. Progress is being shown with this model [15, 16], and purification and reconstitution of some receptors is a definite possibility. In fact, reconstitution of isolated plasma membranes into phospholipids at tips of patch electrodes has been reported, and stimulus-activated cation channels were observed [17]. It is, therefore, imperative that the amount and reactivity of the membrane lipids be assessed in order to provide a basis for the experiments that will seek understanding of the molecular details of reception and transduction. Consequently, we report here the lipid composition of the taste epithelia of the main taste receptor organ of the catfish – the maxillary barbels – and the incorporation of the metabolic substrate, acetate, into the major lipid classes.

Materials and methods

Solutions. Krebs-Ringer bicarbonate solution was made to the following component concentrations: NaCl, 120 mM; KCl, 4.75 mM; $CaCl_2$, 1.2 mM; $MgSO_4$, 1.2 mM; KH_2PO_4, 0.12 mM; $NaHCO_3$, 25.9 mM; pH 7.4. Lipid standards were purchased from Applied Sciences, State College, PA and tested for purity by chro-

matography (several aliquots were tested), as described below. In no instance did the level of impurities exceed 1% and in most instances, no detectable impurities were present. 1-[^{14}C]Acetate was a product of DuPont-NEN. Chloroform and methanol were of HPLC-grade purity. Hyamine solution was purchased from Sigma. All other chemicals were reagent grade.

Collection of epithelial tissues for lipid analysis. Catfish (*Ictalurus punctatus*), weighing 500–1100 g, were purchased from commercial suppliers and maintained at 17 °C in 250-gallon aquaria for not longer than 2 days. Animals were sacrificed by a sharp blow to the neurocranium using a heavy bar. Maxillary barbels from the channel catfish were immediately cut from the animal using a scissor and directly immersed in liquid nitrogen. They were transferred rapidly to the interior of a cryostat (−25 °C) where the epithelial layer of each edge of each barbel was removed by scraping with a scalpel. Care was taken to remove only the epithelial layer rich in taste buds and not the underlying cell layers, nerves and blood vessels. Scraping was performed inside the cryostat with material transferred to cold Folch reagent (chloroform/methanol; 2:1, v/v). After the tissue was collected, the vials were capped and vigorously agitated. Each vial was then placed at −15 °C until analytical procedures were begun (12–18 h).

^{14}C-Acetate incorporation studies. Maxillary barbels were removed from the sacrificed animals and cut into thirds. The upper third, closest to the head, was discarded. The middle third and the tip one third were placed separately into petri dishes containing cold (4 °C) Krebs-Ringer bicarbonate buffer. After several of these portions were collected from five fish (total of 10 barbel sections in each dish), they were cut into small (0.5–2 mm) pieces using a scalpel. The collection of cut pieces of each third of the barbel was then divided into four equal aliquots. Each aliquot was transferred to a Warburg reaction vial containing 2 ml Krebs-Ringer bicarbonate. The center well of the Warburg vessel contained a fan-folded piece of filter paper (Whatman No. 1) soaked in hyamine solution. Vials were flushed with 100% oxygen for 3 s, followed by the addition of 10 µCi of 1-[^{14}C]acetate (1 mCi/mmole) to the vials. Immediately from two of the vials the filter paper was removed and 8 ml of the Folch reagent added. Tissue and solution from these two vials were transferred to a storage vial, vigorously agitated and placed at −15 °C. The other two vials were incubated at 37 °C for 1 h.

Following incubation, the filter paper was removed and 8 ml of Folch reagent was added to each vial. Tissues and solution were transferred to a storage vial after the addition of Folch reagent, vigorously agitated and maintained at −15 °C until the analytical procedures were begun (12 h).

Analytical procedures. All lipids or solutions containing lipids were stored in the presence of ca. 5 µg of butylated hydroxytoluene (BHT) per mg of lipid. Tissue specimens were chopped finely and homogenized in all-glass piston homogenizers; they were extracted with 100 ml of chloroform/methanol (2:1, v/v). Two extractions were required to insure that no lipid was left unextracted. Residues were transmethylated [18] and a subsequent lipid extract performed. No additional lipid material was recovered. Repeated extractions did not yield additional lipid material.

One aliquot of the extract was subjected to silicic acid (Bio-Sil A, 100–200 mesh) column chromatography to separate neutral lipids (by chloroform elution) from phospholipids (by methanol elution). Aliquots of each fraction were then subfractionated into the major lipid classes using TLC as described previously [19]. After visualization of lipids by staining with iodine vapor, the appropriate spots were scraped off, charred by heating with concentrated sulfuric acid and subsequently quantitated by spectrophotometric analysis at 375 nm and compared with known standards obtained in the same manner [20–22]. The amounts of each lipid class were calculated by reference to a standard curve prepared by charring of these known lipid standards. The sum of the charring data of all fractions was considered equal to 100%, and the results for each lipid class are expressed in terms of percentages of total lipid [21, 22].

Plasmalogens were determined on separate samples using the frozen tissue collection procedure described above. The method used was based on the iodine addition procedure [23, 24]. Total phosphorus was performed by the method of Chen et al. [25] and protein was determined by the biuret reaction [26].

To quantitate the amount of ^{14}C incorporated into each TLC fraction, each spot was scraped off the plate, extracted and divided into two equal portions. One portion was subjected to scintillation counting using a Packard Tricarb Scintillation Counter. Data is presented as percent of total radioactivity incorporated into the extracted sample. The other portion was used for total lipid analysis by charring and spectrophotometric assay as described above.

Results and discussion

Results of the total lipid analyses are shown in table 1. Neutral lipids accounted for 38 ± 1% of the total, polar lipids for 62 ± 1%. Of the phospholipids, phosphatidylcholines, phosphatidylserines and phosphatidylethanolamines accounted for the majority, while inositols were lower. This general profile was also noted in another taste-related tissue from the bovine tongue [19]. Plasmalogen levels were relatively high, though not unusual when compared to neural tissue [24]. A previous analysis of bovine lingual taste tissues also revealed relatively high levels of plasmalogens in this chemosensory tissue [24].

The fact that all major lipid classes, with the exception of sphingomyelins, incorporated measurable ^{14}C-acetate indicates that the barbel organ of the catfish contains the

Table 1. Lipid composition of catfish taste epithelium[a, b]

Constituent lipid	% of total lipid
Neutral lipids	
Free fatty acids	5.88
Mono- and diacylglycerols	1.94
Triacylglycerols	6.93
Methyl esters	1.46
Cholesterol	18.81
Cholesteryl esters	2.47
Undetermined	0.91
Total neutral lipids	38.40
Polar lipids	
Phosphatidylcholines	13.74
Lysophosphatidylcholines	2.58
Phosphatidylserines	11.61
Phosphatidylinositols	5.17
Phosphatidylethanolamines	12.30
Cardiolipins	7.62
Sphingomyelins	4.74
Phosphatidic acids	1.77
Undetermined	2.07
Total polar lipids	61.60
Total plasmalogen[c] −0.233 (plasmalogen: P ratio)	

[a] Values are percent of total lipid and represent the average of three independent samples with standard error of the mean of constituents ranging from 0.3 to 2% of total lipid.
[b] Average total lipid in samples was 20.4 ± 1.6% (mg lipid/mg protein: 0.86/4.36, 1.76/7.85, 1.31/6.96).
[c] Total plasmalogens were determined in a separate assay sample. The value is expressed here as the ratio of total plasmalogen to total lipid phosphorus. Amounts are variable, perhaps depending upon such factors as time of year, size of animal, source, diet, etc. Values have ranged from a low of 0.139 to a high of 0.352.

enzymes for de novo, scavenger, or rearrangement pathways (e.g., transesterification) for production of each major lipid (table 2). Of the ^{14}C-acetate added to the tissue, approximately 10% was oxidized to $^{14}CO_2$ and trapped in hyamine. Of the remainder, less than 1% was incorporated into lipids. Of that portion incorporated into the product, the percentages incorporated into lipid are shown in table 2. Table 2 also presents the percent total lipid determined both without (at zero time) incubation and after 60-min incubation of this tissue with ^{14}C-acetate. Comparison of these two values of percent lipid shows a major increase in the triacylglycerol fraction and a decrease in the cholesterol fraction in tissues from the barbel tip portion. This pattern was not observed in the mid-third region of the barbel. Decreases in phosphatidylcholines, phosphatidylserines, phosphatidylinositols and cardiolipins were also noted in both tissue sets with time of incubation. The data indicate that on the basis of ^{14}C incorporation per percentage amount of lipid after 1-h incubation, the polar fraction was more active in its turnover. Values of ^{14}C-acetate incorporation from analysis of the barbel tip when compared with those from barbel mid region were generally similar.

In a separate study, incorporation of ^{14}C-acetate into plasmalogen was determined after a 60-min incubation. Methods were identical to those used to obtain results presented in table 2, with the exception that tissue slices

Table 2. Incorporation of ^{14}C-acetate into lipids in two regions of catfish (barbel) taste epithelium after 60-min incubation and lipid analyses after and before that incubation[a]

Constituent lipid	Barbel tip[b]			Barbel mid-region[c]		
	% ^{14}C	Composition		% ^{14}C	Composition	
		% Lipid at 60 min[d]	% Lipid at zero[e]		% Lipid at 60 min[d]	% Lipid at zero[e]
Neutral lipids						
Free fatty acids	12.1	6.3	5.9	15.2	8.9	6.0
Mono- and diacylglycerols	7.8	6.8	3.4	4.5	4.6	3.0
Triacylglycerols	3.1	22.2	7.6	3.9	9.8	8.3
Methyl esters	0.6	3.6	1.2	0.3	4.2	1.1
Cholesterol	5.4	7.2	16.4	4.0	16.1	16.2
Cholesteryl esters	0.6	9.5	4.2	0.4	7.6	5.8
Undetermined	0.9	11.1	5.1	0.5	8.8	0.9
Polar lipids						
Phosphatidylcholines	16.2	8.3	11.8	21.9	4.9	13.9
Lysophosphatidylcholines	trace	trace	3.2	trace	trace	4.0
Phosphatidylserines	12.8	2.0	9.7	13.3	4.1	11.1
Phosphatidylethanolamines	28.2	15.3	13.2	23.5	17.6	12.9
Phosphatidylinositols	4.3	1.7	4.2	5.3	3.5	5.4
Cardiolipins	1.7	1.1	5.9	1.6	1.0	5.2
Sphingomyelins	trace	2.0	3.0	trace	2.4	2.2
Phosphatidic acids	4.3	2.0	1.9	2.7	4.3	2.8
Undetermined	1.7	1.0	3.3	2.7	2.1	1.4

[a] Values are from a single experiment with two vials of material per each time point receiving ^{14}C-acetate. Each of these vials was analyzed in duplicate. Thus, the values in this table are the result of quadruplicate analyses.
[b] Average total incorporated radioactivity in tip samples was 12.805×10^3 dpm, of which 3.908×10^3 was in the neutral lipid fraction and 8.897×10^3 dpm was in the polar lipid fraction. Average total protein was 8.57 mg.
[c] Average total incorporated radioactivity in mid-region was 6.094×10^3 dpm, of which 1.761×10^3 dpm was in the neutral lipid fraction and 4.288×10^3 dpm was in the polar lipid fraction. Average total protein was 10.48 mg.
[d] The percent of total lipid for each fraction determined after 60-min incubation of the tissue fractions in the presence of acetate. These are averages of two vials with error estimated between 1.0 and 3.0%.
[e] Percent total lipid for each fraction determined at zero time.

from the tip and mid barbel regions were combined. Results indicated that ^{14}C-acetate was incorporated into plasmalogen in both the phosphatidylethanolamine (PE) and phosphatidylcholine (PC) classes. Incorporation of ^{14}C-acetate into PE-plasmalogen amounted to 2.0% of the radioactivity in total phospholipids and 20.1% of the radioactivity in total PE. Chemical analysis by two-dimensional TLC followed by phosphate assay [24] indicated that PE-plasmalogen comprised 69.4% of total PE. Incorporation of ^{14}C-acetate into PC-plasmalogen amounted to 0.8% of the radioactivity in total phospholipids and 5.2% of the radioactivity in total PC. Chemical analysis of this sample demonstrated that PC-plasmalogen comprised 5.3% of the total PC.

Previous lipid analyses of taste sensory epithelia have revealed profiles similar to those from non-sensory epithelia [19]. Data in table 1 from catfish maxillary barbel sensory epithelia show a similar profile. Free fatty acids are relatively low (even after 1 h of incubation) suggesting a low activity of general lipases or a high level of scavenger pathways. Lipase activity was found to be high in steer lingual tissue but could be inhibited by lidocaine [27]. Lidocaine addition was not necessary for the present studies. In catfish barbel epithelia, phosphatidylcholines, phosphatidylserines and phosphatidylethanolamines accounted for the higher percentages of phospholipids, with inositols accounting for a lower portion. In the steer taste tissue [19], phosphatidylcholines and ethanolamines were higher than either phosphatidylserines or phosphatidylinositols. The level of phosphatidylinositols is normal compared with most other tissues. Metabolism of this lipid has been suggested as a transductive sequence in taste reception [28].

Plasmalogen content is relatively high in this taste tissue (table 1) as it was in the steer taste tissue [24]. Plasmalogen was detected in both the phosphatidylcholine (PC) and phosphatidylethanolamine (PE) fraction. In general, using epithelial scrapings, the PC plasmalogen accounted for about 30% of the total plasmalogen, the PE plasmalogen for about 70%. The amount of plasmalogen was somewhat variable ($\pm$15–20%) depending on individual animals sampled and, perhaps, season of the year, but it was always found that the majority of the total of the PC plus PE fraction was in the plasmalogen form. Whether or not this level of plasmalogen has a functional role to play in taste transduction remains to be explored. Irvine et al. have reported an increase in phospholipase C activity derived from rat brain with exogenous addition of phosphatidylethanolamines [29]. We have also observed an increase in phospholipase C activity from catfish barbel taste tissue with exogenous addition of plasmalogen-enriched PE compared to phosphatidylethanolamines from either soybean or a synthetic source (neither of which contain plasmalogen) (Huque and Brand, unpublished observations).

Incubation of the barbel tissue results in an apparent shift in lipid profile. Note that in the data of table 2, total tissue (i.e., epithelia, vessels, nerves, connective tissue) was analyzed. Higher levels of triacylglycerols and lower levels of free cholesterol were consistently observed in all of the samples from the barbel tip region after incubation. The high level of undetermined lipids from this neutral fraction could be masking a higher level of unidentified cholesterol esters. We have segregated tissue from the tip from that of mid-region in these studies because the tip region shows a greater density of taste buds and is an active site of development of new buds. In fact, for this study, little difference was noted in percentages between the two, with the exception of the triacylglycerol and cholesterol fractions.

The ability of this tissue to incorporate ^{14}C-acetate into individual lipid classes was determined after 60-min incubation. These incorporations could be due to synthesis of individual lipids and fatty acids de novo and to rearrangements, transesterifications, etc., of one lipid class to another. The free fatty acid fraction, while low on a chemical percentage basis, is nevertheless fairly heavily labeled by ^{14}C. Since the phospholipid fractions are also heavily labeled, on the basis of percentage amounts, it is probable that phospholipases are active in generating these free fatty acids and mono- and diacylglycerols. Phospholipases are known to be active in the olfactory sensory tissues of this animal [30].

This study has presented the lipid profile of taste sensory epithelia from catfish barbel permitting artificial lipid mixes to be formulated for reconstitution studies. The study has also demonstrated that this tissue is capable of incorporating the acetate into almost all lipid classes, thus confirming that it is a metabolically active organ.

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Sex pheromone conversion and degradation in antennae of the silkworm moth *Bombyx mori* L.

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Dedicated to Professor Adolf Butenandt on the occasion of his 85th birthday

Summary. In living antennae of the silkworm moth *Bombyx mori* L. the pheromone compound (*E, Z*)-10,12-hexadecadienol and hexadecanol are enzymatically converted to their corresponding fatty aldehydes, acids and long-chain fatty acid esters. The pheromone is completely degraded at high rates in the antennae of freshly hatched moths. The polar volatile [^{3}H]metabolites exclusively consist of tritiated water. The half-life of the pheromone is about 2.5 min in males and 0.5 min in females. Drying inactivates the enzymes responsible for pheromone oxidation.
Key words. Lepidoptera; *Bombyx mori* L.; moths; antennae; pheromones; metabolites; enzymes.

Introduction

Fifty years ago, Adolf Butenandt described chemical experiments with sex attractants obtained from abdominal glands (sacculi lateralis) of female silkmoths of *Bombyx mori* L.[1]. The main pheromone component, bombykol, was identified later as a long-chain and double unsaturated fatty alcohol: (*E, Z*)-10,12-hexadecadien-1-ol (*E*10, *Z*12-16:ol)[2,3]. An historical retrospect on this pioneering work was given by Hecker and Butenandt[4]. The domestic silkworm *Bombyx mori* L. belongs to the most widely used and investigated species of silkworms, which has been cultivated in China for more than four thousand years[5].

The pheromone isomer (*E, E*)-10,12-hexadecadien-1-ol and the component (*E, Z*)-10,12-hexadecadien-1-al (bombykal: *E*10, *Z*12-16:Al) were also found in gland extracts of the female moths of *Bombyx mori* L.[6–8]. Studies on pheromone metabolism began after the synthesis of bombykol and its labeling to [^{3}H]bombykol[9].

Pheromone uptake and transformation in the antennae of *Bombyx mori* L. begins with the adsorption of the airborne molecules on the long sensory hairs of the antennae[10,11]. The adsorbed molecules reach the cuticular pores and pore tubuli by two-dimensional diffusion along the epicuticle of the sensilla surface[12,13]. It is probable that they diffuse through the pore tubuli towards the dendritic membranes of the receptor cells. Bombykol molecules also migrate along the outer hair surface or within the hair lumen towards the branches of the antennae. Presumably, some molecules penetrate through the cuticular pores of the antennal branches into the cells and hemolymph[14].

It was suggested that interaction of pheromone molecules with proposed receptor-molecules of the dendritic membranes is followed by rapid inactivation[15]. Time courses of electrophysiological responses indicate that the pheromone molecules must be inactivated within seconds after the excitatory interactions, whereas the half-lives of pheromone conversion were found in the order of some minutes[16]. Therefore, inactivation by enzymatic metabolism is not identical with the previously postulated rapid inactivation mechanism[17].

Investigations on the enzymatic conversion of bombykol in *Bombyx mori* L. were initially performed with [12,13-^{3}H] (*E, Z*)-10,12-hexadecadien-1-ol [^{3}H]bombykol. Tritiated bombykol and homologous fatty alcohols applied onto antennae of moths were oxidized to long-chain fatty acids and, to a small extent, esterified to fatty acid esters[18].

This paper reports on the pheromone conversion and degradation using [^{3}H]bombykol as the pheromone