

## The Effect of Olfactory Deprivation on the Thresholds of Sensitivity of Skin Chemoreceptors of Carp *Cyprinus carpio*

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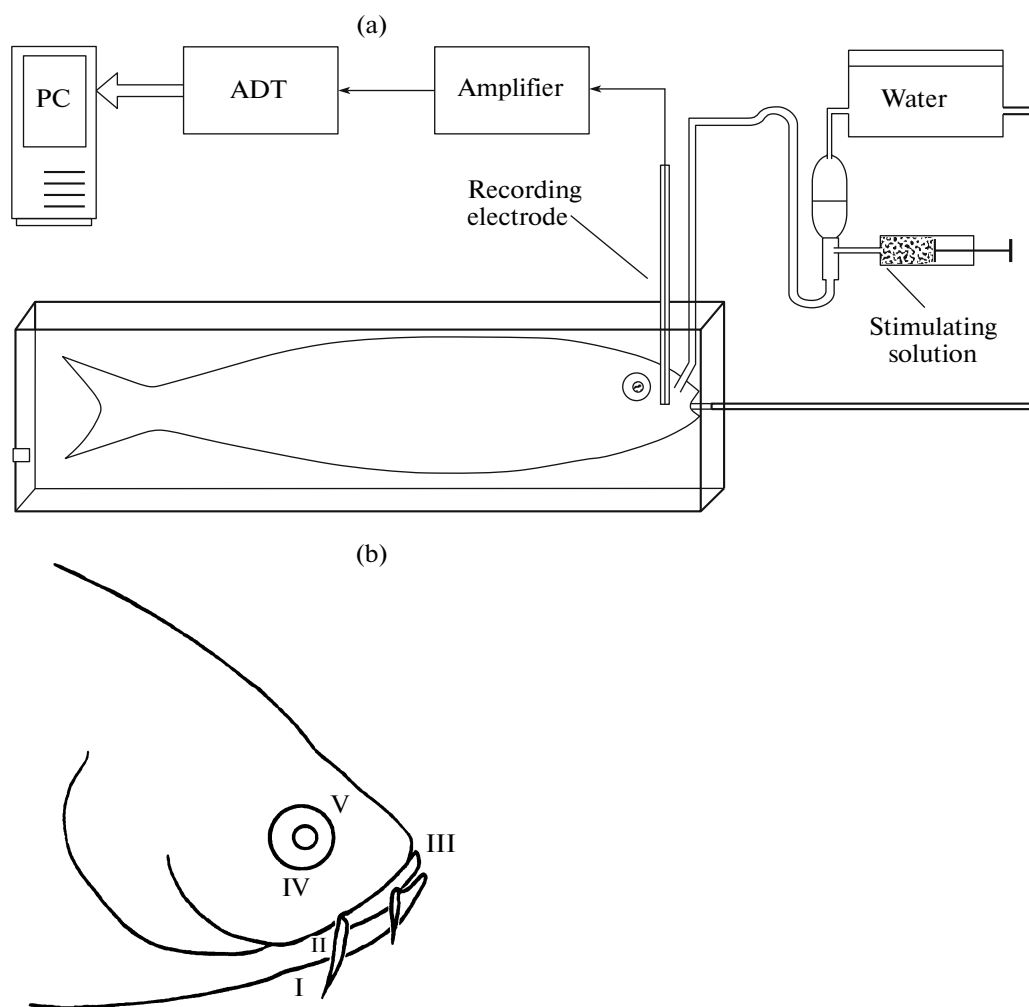
**Abstract**—Using method of registration of electrical potentials caused by chemical stimulation of the skin surface of the head of the carp *Cyprinus carpio*, the effect of prolonged olfactory deprivation (3, 9, and 12 months after operation) and partial blinding of anosmiated fish (9 months) on the sensitivity thresholds of external chemoreceptors was studied. It was found that, 3 months following anosmiation, the thresholds decreased by orders of 0.1–0.5, and, after 9 and 12 months, they decreased by orders of 0.1–0.8 depending on the kind of the chemical stimulus and the zone of registration. The highest increase in the sensitivity of skin chemoreceptors was recorded in anosmiated fish deprived also of object vision, by orders of 0.3–1.5. The results obtained indicate the existence of a close functional relationship between the olfactory and visual systems, on the one hand, and the skin chemosensory system, on the other hand. The compensatory processes taking place in these systems in the case of the loss of one of them have an adaptive pattern and are directed at provision of reliability of behavioral contacts and survival of fish in the environment.

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**Key words:** skin chemoreception, chronic anosmia, compensatory interaction of sensory systems, fish.

In nature, the animal makes a decision and performs the respective behavioral acts, for instance, search for food, relying on the integrated information coming from many sensory systems (Pavlov and Kasumyan, 1990). The polysensory afferent synthesis is the basis of formation of adequate responses of animals to signals coming from the outside. The rapid recognition of biologically important substances present in water is an essential condition for efficient adaptation to changes occurring in the environment. In fish, the reception of chemical stimuli dissolved in water is exercised thanks to olfaction, the gustatory system, single chemosensory cells, and free nerve endings of cranial and spinal nerves (Whitaker, 1971, 1992; Gomahr et al., 1992; Kasumyan et al., 1999). Gustatory reception whose morphological substrate are taste buds is of key importance in the ability of fish to localize and select food objects (Atema, 1971). It is separated into two subsystems: extraoral, represented by taste buds on the head, body, and fins and mediated by the facial nerve; and intraoral represented by taste buds in the oral cavity and mediated by facial, vagus, and glossopharyngeal nerves. The first of them provides food localization in the environment, and the information from the second is decisive for triggering the response of swallowing or rejection of food (Finger, 1997; Kasumyan and Døving, 2003).

The interaction of individual chemosensory systems and the lability of exterochemoreception in fish are indicated by data of morphological, electrophysiological and behavioral studies (Chervova and Lapshin, 2005; Devitsina, 2006; Kasumyan and Marusov, 2007). The processes of convergence of multimodal afferentations in brain structures of fish, such as tectum opticum, to which fibers from the visual and olfactory analyzers, acoustico-lateral system, and skin reception are projected (Airapet'yants and Batuev, 1969) and habenula having contacts with visual and olfactory centers (Devitsina and Marusov, 2007), are apparently a prerequisite for the compensatory increase in the activity of intact receptor systems at the damage of one of the sensory modalities. It was shown that, in some fish species having external taste buds, including Cyprinidae, after prolonged olfactory deprivation (anosmia), the sensitivity for odors can restore at the expense of the compensatory development of external gustatory reception (Kasumyan and Marusov, 2002, 2003, 2007; Kasumyan et al., 2005). However, several important issues cannot be considered sufficiently elucidated, for instance, whether functional transformations occur in skin chemoreception caused by anosmia and blinding and what the nature of these changes is. Studies of the intraoral gustatory system demonstrated that in fish spectra of taste preferences and threshold concentrations of taste stimuli after chronic anosmia did not differ from those in the norm



**Fig. 1.** (a) Scheme of the unit for recording thresholds of sensitivity of external chemoreceptors to solutions of chemical substances and (b) the zone of recording sensitivity of external chemoreceptors. Designations: ADT is analog-digital transformer; PC is personal computer; (I) gular region; (II) base of big barbel; (III) middle of the upper lip; (IV) infraorbital region; (V) interorbital space.

(Kasumyan and Sidorov, 2005). The experimental material on the study of interaction and complementarity of chemosensory systems accumulated up to the present time does not contain data on changes in the thresholds of sensitivity of external chemoreceptors in fish after chronic anosmia and visual deprivation.

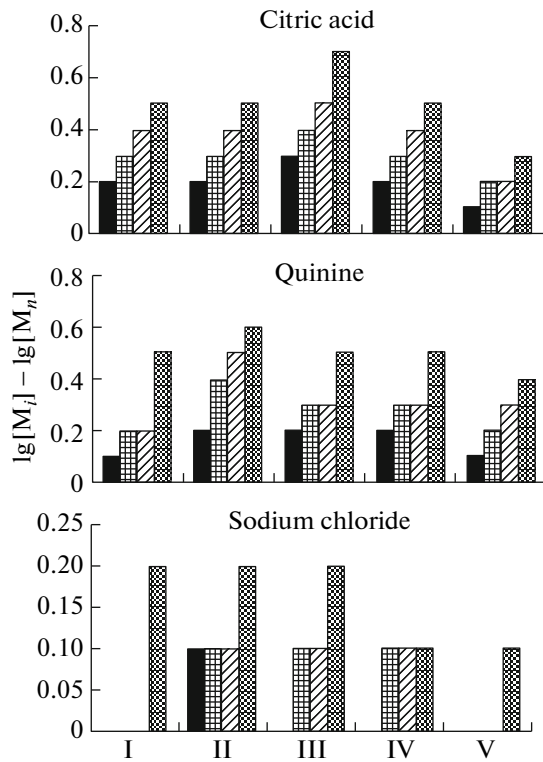
The purpose of our work was to study time dynamics of sensitivity of skin chemoreceptors in fish in the framework of compensatory intersystemic sensory interactions.

## MATERIAL AND METHODS

Experiments were performed in autumn and winter on two-year-old carps *Cyprinus carpio* with a length of 15–20 cm and a weight of 50–100 g kept in laboratory aquariums at temperatures 18–20°C and fed on live food (midge). A total of 30 fish were used.

Fish were anosmiated using the method of bilateral thermocauterization of the olfactory epithelium (Kasumyan and Marusov, 2002). Fish were taken for experiments 3, 9, and 12 months after anosmiation operation. On control animals, an operation of false anosmiation was performed—a small site of skin near the olfactory rosette was cauterized. A separate series of experiments was performed also on anosmiated fish with a removed eye lens.

As test chemical stimuli, solutions  $10^{-8}$ – $10^{-2}$  M L-amino acids of cysteine, histidine, phenylalanine, and proline, as well as solutions of classic taste substances quinine-hydrochloride  $5 \times 10^{-6}$ – $5 \times 10^{-3}$  M, sodium chloride, and citric acid  $10^{-5}$ – $5 \times 10^{-3}$  M, and saccharose  $5 \times 10^{-3}$ – $5 \times 10^{-1}$  M were used. Tap water that for no less than 24 h settled in the reservoir served as solvent and control. The interval between individual deliveries was 2 min. The sequence of substance delivery was changed in an arbitrary manner.



**Fig. 2.** Change in thresholds of sensitivity in the carp *Cyprinus carpio* to amino acids and classic taste substances as a result of anosmia of different duration ( $\lg[M_i]$ ), as compared to intact ( $\lg[M_n]$ ). Designations of individuals: (■) anosmiated 3 months; (▨) anosmiated 9 months; (▩) anosmiated 12 months; (▧) anosmiated and deprived of vision 9 months; see Fig. 1b for the remaining designations.

Fish were fixed in a unit so that all of their body was in the water, except the upper part of the head covered with moist tissue. Gills were constantly watered with running water from the settling tank (rate of 150 ml/min at temperatures of 18–20°C) (Fig. 1a). No muscle relaxants and anesthetics were used. After experiments, fish released into the aquarium continued to swim and feed as usual.

Slow electric potentials in five zones of the carp head zone (Fig. 1b) in response to the local delivery of the chemical substance solution were recorded. As a recording electrode, a silver chlorinated wire located within a glass capillary filled with water and adjusted from the butt end on the skin surface was used. Fluctuations of the electric potential reflected summary responses of skin chemoreceptors to the adequate stimulation.

The subsequent data processing included calculation of the average from algorithms of values of threshold concentrations. The degree of change of thresholds was assessed as a difference of logarithms of threshold concentrations after operations ( $\lg[M_i]$ ) and in the norm ( $\lg[M_n]$ ).

The conclusion of the significance of differences of values of thresholds measured in operated and intact fish was verified using Wilcoxon nonparametric  $U$ -test at the action of one type of substance. If it is not specially specified in the text, it is implied that the compared groups of results passed the test for significance.

The procedure of stimulation by near-threshold stimuli of skin receptors and simultaneous registration of their responses were previously described (Cherova and Lapshin, 2005).

## RESULTS

The sensitivity thresholds of anosmiated carps to test substances turned out to be lower than in the control group (table): already in 3 months after anosmia the thresholds in all five zones decreased by orders of 0.1–0.2 ( $p > 0.05$ ) and 0.3–0.5 ( $p > 0.05$ ) and in 9 and 12 months by 0.1–0.2 ( $p > 0.05$ ) and by 0.3–0.8 ( $p > 0.05$ ) depending on the substance and the zone of recording. The sensitivity thresholds in false-anosmiated fish did not differ from those in the norm (Fig. 2).

Still more noticeable increase in the sensitivity of skin receptors was recorded in anosmiated fish simultaneously deprived of object vision, by orders of 0.3–1.5 ( $p < 0.05$ ). This effect was most pronounced in three most sensitive zones: near upper-jaw barbel (zone II, Fig. 1b), in the gular zone (zone I), and at the upper mouth fold (zone III). In the interorbital area (zone V), a significant decrease in thresholds to all substances was recorded not earlier than at 6–9 months. In anosmiated fish, the most pronounced effect of decrease in thresholds to amino acids was observed for cysteine, and the lowest was observed for proline. Of classic taste substances, during anosmia thresholds decreased maximum to citric acid ( $p < 0.05$ ); no changes in thresholds were revealed to sodium chloride and to saccharose (table, Fig. 2).

## DISCUSSION

The results obtained in the present study suggest the presence of a close relationship between the olfactory, visual, and skin chemoreceptor systems in the carp. The decrease of sensitivity thresholds of external chemoreceptors in the carp to amino acids and taste substances after anosmia and partial blinding with great probability is the manifestation of compensatory processes taking place at the level of central brain formations to which afferents of the respective analyzers are projected. These processes determine the flexibility of sensory systems, i.e., the capacity for rearranging their functional characteristics depending on the changed needs of the body, for instance, in the cases of need in the compensation of the lost function at the periphery (Flerova, 1983).

This flexibility is also evidenced by our experiments. Three months after anosmia operation, the sensitivity thresholds to cysteine in the area of the base

Average values of thresholds of sensitivity of external chemoreceptors in intact (according to data of Chervova and Lapshin, 2005) and anosmiated carps *Cyprinus carpio* 3, 9, and 12 months after operation

Tested individuals	Zones of recording				
	I	II	III	IV	V
			Cysteine, M		
Intact	10 <sup>-4.4</sup>	10 <sup>-5.2</sup>	10 <sup>-4.3</sup>	10 <sup>-3.1</sup>	10 <sup>-2.5</sup>
False-anosmiated	10 <sup>-4.4</sup>	10 <sup>-5.2</sup>	10 <sup>-4.3</sup>	10 <sup>-3.1</sup>	10 <sup>-2.5</sup>
Anosmiated, 3 months	10 <sup>-4.7</sup>	10 <sup>-5.7</sup>	10 <sup>-4.7</sup>	10 <sup>-3.4</sup>	10 <sup>-2.6</sup>
Anosmiated, 9 months	10 <sup>-4.9</sup>	10 <sup>-6.0</sup>	10 <sup>-5.0</sup>	10 <sup>-3.7</sup>	10 <sup>-2.8</sup>
Anosmiated, 12 months	10 <sup>-4.9</sup>	10 <sup>-6.0</sup>	10 <sup>-5.0</sup>	10 <sup>-3.7</sup>	10 <sup>-2.8</sup>
Anosmiated and deprived of vision, 9 months	10 <sup>-5.6</sup>	10 <sup>-6.7</sup>	10 <sup>-5.7</sup>	10 <sup>-4.0</sup>	10 <sup>-3.2</sup>
			Phenylalanine, M		
Intact	10 <sup>-4.2</sup>	10 <sup>-5.0</sup>	10 <sup>-4.7</sup>	10 <sup>-2.5</sup>	10 <sup>-2.3</sup>
False-anosmiated	10 <sup>-4.2</sup>	10 <sup>-5.0</sup>	10 <sup>-4.7</sup>	10 <sup>-2.5</sup>	10 <sup>-2.3</sup>
Anosmiated, 3 months	10 <sup>-4.5</sup>	10 <sup>-5.4</sup>	10 <sup>-5</sup>	10 <sup>-2.7</sup>	10 <sup>-2.4</sup>
Anosmiated, 9 months	10 <sup>-4.7</sup>	10 <sup>-5.6</sup>	10 <sup>-5.2</sup>	10 <sup>-2.9</sup>	10 <sup>-2.5</sup>
Anosmiated, 12 months	10 <sup>-4.7</sup>	10 <sup>-5.6</sup>	10 <sup>-5.2</sup>	10 <sup>-2.9</sup>	10 <sup>-2.5</sup>
Anosmiated and deprived of vision, 9 months	10 <sup>-5.3</sup>	10 <sup>-6.3</sup>	10 <sup>-5.9</sup>	10 <sup>-3.2</sup>	10 <sup>-2.8</sup>
			Histidine, M		
Intact	10 <sup>-3.5</sup>	10 <sup>-4.7</sup>	10 <sup>-4.5</sup>	10 <sup>-3.3</sup>	10 <sup>-2.3</sup>
False-anosmiated	10 <sup>-3.5</sup>	10 <sup>-4.7</sup>	10 <sup>-4.5</sup>	10 <sup>-3.3</sup>	10 <sup>-2.3</sup>
Anosmiated, 3 months	10 <sup>-3.7</sup>	10 <sup>-5.0</sup>	10 <sup>-4.8</sup>	10 <sup>-3.6</sup>	10 <sup>-2.4</sup>
Anosmiated, 9 months	10 <sup>-4.0</sup>	10 <sup>-5.1</sup>	10 <sup>-4.9</sup>	10 <sup>-3.7</sup>	10 <sup>-2.5</sup>
Anosmiated, 12 months	10 <sup>-4.0</sup>	10 <sup>-5.2</sup>	10 <sup>-4.9</sup>	10 <sup>-3.7</sup>	10 <sup>-2.6</sup>
Anosmiated and deprived of vision, 9 months	10 <sup>-4.5</sup>	10 <sup>-5.9</sup>	10 <sup>-5.7</sup>	10 <sup>-4.0</sup>	10 <sup>-2.7</sup>
			Proline, M		
Intact	10 <sup>-4.0</sup>	10 <sup>-4.4</sup>	10 <sup>-4.3</sup>	10 <sup>-1.8</sup>	10 <sup>-1.5</sup>
False-anosmiated	10 <sup>-4.0</sup>	10 <sup>-4.4</sup>	10 <sup>-4.3</sup>	10 <sup>-1.8</sup>	10 <sup>-1.5</sup>
Anosmiated, 3 months	10 <sup>-4.1</sup>	10 <sup>-4.7</sup>	10 <sup>-4.5</sup>	10 <sup>-1.9</sup>	10 <sup>-1.7</sup>
Anosmiated, 9 months	10 <sup>-4.2</sup>	10 <sup>-4.9</sup>	10 <sup>-4.6</sup>	10 <sup>-2.1</sup>	10 <sup>-1.8</sup>
Anosmiated, 12 months	10 <sup>-4.2</sup>	10 <sup>-4.9</sup>	10 <sup>-4.7</sup>	10 <sup>-2.2</sup>	10 <sup>-1.9</sup>
Anosmiated and deprived of vision, 9 months	10 <sup>-4.4</sup>	10 <sup>-5.0</sup>	10 <sup>-4.9</sup>	10 <sup>-2.3</sup>	10 <sup>-2.0</sup>
			Citric acid, M		
Intact	10 <sup>-3.7</sup>	10 <sup>-3.7</sup>	10 <sup>-3.7</sup>	10 <sup>-3.3</sup>	10 <sup>-3.3</sup>
False-anosmiated	10 <sup>-3.7</sup>	10 <sup>-3.7</sup>	10 <sup>-3.7</sup>	10 <sup>-3.3</sup>	10 <sup>-3</sup>
Anosmiated, 3 months	10 <sup>-3.9</sup>	10 <sup>-3.9</sup>	10 <sup>-4.0</sup>	10 <sup>-3.5</sup>	10 <sup>-3.4</sup>
Anosmiated, 9 months	10 <sup>-4.0</sup>	10 <sup>-4.0</sup>	10 <sup>-4.1</sup>	10 <sup>-3.6</sup>	10 <sup>-3.5</sup>
Anosmiated, 12 months	10 <sup>-4.1</sup>	10 <sup>-4.1</sup>	10 <sup>-4.2</sup>	10 <sup>-3.7</sup>	10 <sup>-3.5</sup>
Anosmiated and deprived of vision, 9 months	10 <sup>-4.2</sup>	10 <sup>-4.2</sup>	10 <sup>-4.4</sup>	10 <sup>-3.8</sup>	10 <sup>-3.6</sup>
			Quinine, M		
Intact	10 <sup>-4.0</sup>	10 <sup>-4.1</sup>	10 <sup>-4.3</sup>	10 <sup>-3.3</sup>	10 <sup>-3.0</sup>
False-anosmiated	10 <sup>-4.0</sup>	10 <sup>-4.1</sup>	10 <sup>-4.3</sup>	10 <sup>-3.3</sup>	10 <sup>-3.0</sup>
Anosmiated, 3 months	10 <sup>-4.1</sup>	10 <sup>-4.3</sup>	10 <sup>-4.5</sup>	10 <sup>-3.5</sup>	10 <sup>-3.1</sup>
Anosmiated, 9 months	10 <sup>-4.2</sup>	10 <sup>-4.5</sup>	10 <sup>-4.6</sup>	10 <sup>-3.6</sup>	10 <sup>-3.2</sup>
Anosmiated, 12 months	10 <sup>-4.2</sup>	10 <sup>-4.6</sup>	10 <sup>-4.6</sup>	10 <sup>-3.6</sup>	10 <sup>-3.3</sup>
Anosmiated and deprived of vision, 9 months	10 <sup>-4.5</sup>	10 <sup>-4.7</sup>	10 <sup>-4.8</sup>	10 <sup>-3.8</sup>	10 <sup>-3.4</sup>
			Sodium chloride, M		
Intact	10 <sup>-3.1</sup>	10 <sup>-3.0</sup>	10 <sup>-3.3</sup>	10 <sup>-3.0</sup>	10 <sup>-3.2</sup>
False-anosmiated	10 <sup>-3.1</sup>	10 <sup>-3.0</sup>	10 <sup>-3.3</sup>	10 <sup>-3.0</sup>	10 <sup>-3.2</sup>
Anosmiated, 3 months	10 <sup>-3.1</sup>	10 <sup>-3.1</sup>	10 <sup>-3.3</sup>	10 <sup>-3.0</sup>	10 <sup>-3.2</sup>
Anosmiated, 9 months	10 <sup>-3.1</sup>	10 <sup>-3.1</sup>	10 <sup>-3.4</sup>	10 <sup>-3.1</sup>	10 <sup>-3.2</sup>
Anosmiated, 12 months	10 <sup>-3.1</sup>	10 <sup>-3.1</sup>	10 <sup>-3.4</sup>	10 <sup>-3.1</sup>	10 <sup>-3.2</sup>
Anosmiated and deprived of vision, 9 months	10 <sup>-3.3</sup>	10 <sup>-3.2</sup>	10 <sup>-3.5</sup>	10 <sup>-3.1</sup>	10 <sup>-3.3</sup>
			Saccharose, M		
Intact	10 <sup>-1.5</sup>	10 <sup>-1.8</sup>	10 <sup>-2.0</sup>	10 <sup>-1.0</sup>	10 <sup>-1.0</sup>
False-anosmiated	10 <sup>-1.5</sup>	10 <sup>-1.8</sup>	10 <sup>-2.0</sup>	10 <sup>-1.0</sup>	10 <sup>-1.0</sup>
Anosmiated, 3 months	10 <sup>-1.5</sup>	10 <sup>-1.8</sup>	10 <sup>-2.0</sup>	10 <sup>-1.0</sup>	10 <sup>-1.0</sup>
Anosmiated, 9 months	10 <sup>-1.5</sup>	10 <sup>-1.8</sup>	10 <sup>-2.0</sup>	10 <sup>-1.0</sup>	10 <sup>-1.0</sup>
Anosmiated, 12 months	10 <sup>-1.5</sup>	10 <sup>-1.8</sup>	10 <sup>-2.0</sup>	10 <sup>-1.0</sup>	10 <sup>-1.0</sup>
Anosmiated and deprived of vision, 9 months	10 <sup>-1.5</sup>	10 <sup>-1.8</sup>	10 <sup>-2.0</sup>	10 <sup>-1.0</sup>	10 <sup>-1.0</sup>

Note: I is gular region, II is base of big barbel, III is middle of the upper lip, IV is infraorbital region, and V is interorbital space.

of the big upper-jaw barbel increased by orders of 0.5 to cysteine; 0.2–0.4 to other amino acids; and by 0.1–0.2 to classic taste substances. The sensitivity thresholds to saccharose changed in neither studied zone. In this connection, note that, according to data of several authors (Funakoshi et al., 1981; Chervova and Lapshin, 2005), carps are characterized by a very low sensitivity to saccharose or an indifferent response to the taste of this substance in behavioral experiments (Kasumyan and Morsi, 1996).

According to data of morphological studies (Devitsina, 2006), in the basal part of the big upper-jaw barbel of the carp, the density of taste buds in the norm is minimal (30–40 buds/mm<sup>2</sup>), as compared to its middle part (200–300 buds/mm<sup>2</sup>) and the apex (about 600 buds/mm<sup>2</sup>). It was also shown that, 3 months after anosmiation, the number of taste buds increased at the barbel, on average, by approximately 1.5 times and was retained at this level in the subsequent months. The area of the apical surface of the taste bud increased by 80–90%, and after 9 months increased by another 30%.

The data obtained in the present study, on the whole, agree with the aforementioned morphological measurements: thresholds to the chemical substances used by us 9 months after anosmia operation turned out lower as compared to thresholds after 3-month olfactory deprivation. Twelve months after anosmia, thresholds remained almost at the same level; insignificant changes in the thresholds were observed to the least efficient amino acids (histidine, proline) and classic taste substances (table), which evidences the mosaicism of vicariating processes.

A noticeable decrease in the thresholds was observed in the area of the upper lip and in the gular zone (table, Fig. 2). The study of morphology of these regions in anosmiated carps found their high reactivity to switching off the olfactory reception. In the gular zone, the formation of additional structures of “external taste” as epidermal outgrowths above the lower lip covered with taste buds was noted (Devitsina, 2006).

The fact that, in anosmiated and visually deprived fish, thresholds after 9 months were lower than in only anosmiated fish can be explained apparently by the fact that the deficit of the sensory inflow simultaneously in two afferent systems stimulates triggering of compensatory processes either with a greater intensity or according to another algorithm. The study of the region of projections of the olfactory and visual analyzer systems, as well as of the area of their common representation, demonstrated a vast zone of convergence of different-mode flows in the forebrain of the carp that in the functional respect is comparable to the hippocampal brain cortex of other vertebrates (Nikonov and Obukhov, 1983).

Behavioral experiments on carps with chronic switching off of olfactory reception also demonstrated a functional compensatory activation of the system of external taste reception manifested in fish 1.5–

3.0 months after olfactory deprivation (Kasumyan et al., 2005). In other species of cyprinids, the ability to adequately respond to food odors was partially recovered 3 months after the onset of anosmia, which enables individuals deprived of olfaction to successfully find the source of the chemical signal (Kasumyan and Marusov, 2002).

Thus, we can state that, in anosmiated fish, the greatest compensatory increase in skin sensitivity occurs in those head regions that normally also exhibit high sensitivity to chemical substances (base of the upper-jaw barbel, gular region, and upper mouth fold). It can be assumed that, in anosmiated and simultaneously deprived of object vision fish, compensatory processes proceed with still greater intensity since the destructive impact simultaneously on two receptor systems likely causes a protective intensification of specific activity of other afferent systems of the body. The data obtained indicate functioning of efficient mechanisms of the integrative interaction of sensory systems in fish providing the reliability of formation of adequate behavior under conditions of a deficit of the sensory flow from one or several receptor systems.

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