EXPERIMENTAL PAPERS

A Noninvasive Electrophysiological Investigation of Tactile Sensitivity in Cyprinid Fish (Cyprinidae)

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Abstract—Tactile reception in cyprinid fish (silver crucian carp *Carassius auratus gibelio* and common carp *Cyprinus carpio*) was investigated by noninvasive recording of action potentials from the head skin in response to rhythmic tactile stimulation. Responses shaped as electric potentials following synchronously with changes in the pressure force on the skin were recorded using chlorosilver electrodes. It was shown that fish, like all terrestrial vertebrates, have phasic and tonic tactile receptors. Three main types of tactile responses were distinguished: (1) tonic responses as potential fluctuations repeating the dynamics of the tactile stimulus, (2) phasic responses as on-, off-, and on-off potentials, and (3) slow deflections from the resting potential. Compound responses comprising simultaneously different types of responses were also recorded. The response latency averaging 6.1 ms for tonic and 4.4 ms for phasic responses was clearly independent of the stimulus direction (switch-on, switch-off). The threshold level of tactile sensitivity in the perioral and gular head areas was $0.05-0.2$ g/mm^2. Tactile receptors on the silver crucian carp and common carp heads exhibited zonal distribution patterns, with sensory areas differing in their tactile sensitivity. Most sensitive areas were on the upper and lower lips, in the perilabial skin and the gular area on the ventral side of the head. Less sensitive areas were situated rostrally and ventrally to the eyeball. The areas situated dorsally and caudally to the eyeball proved to be insensitive to the applied tactile stimulation. In all sensory areas on the fish head, most intense responses were evoked by sliding tactile stimuli. The distribution specificity of tactile sensory areas meets their functional significance for fish feeding behavior.

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INTRODUCTION

Fish integument contains numerous sensory structures of different modality, including chemo-, mechano- and electroreception [1—3]. Fish living in low-illumination conditions actively exploit tactile reception in various behaviors. It plays a particularly important role in the orientation system of inhabitants of benthic biotopes and cave reservoirs [3—6]. In vertebrates, the informational
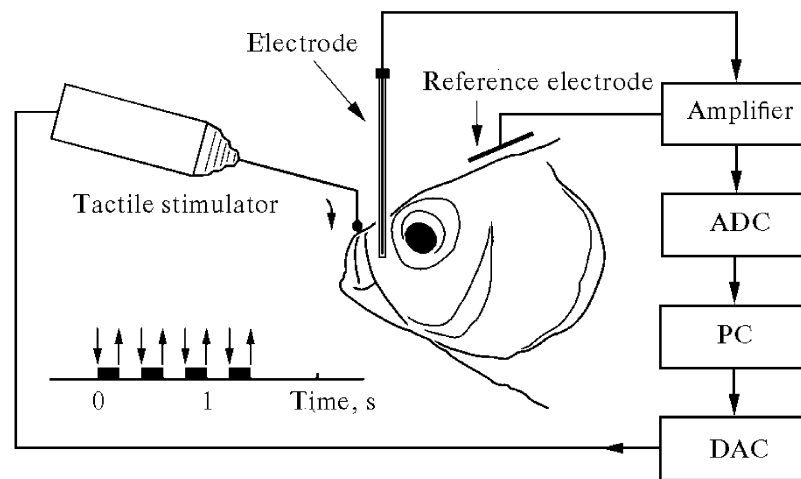
Fig. 1. A setup for measuring tactile sensitivity in fish. The stimulus is applied onto the skin by a computer-controlled tactile stimulator. The electrical response is recorded from the skin through the electrode. Inset diagram shows the sequence of a single stimulation episode. Downward arrows indicate an increase in pressure on the skin, upward arrows show a pressure relief. ADC—analog-to-digital converter; PC—personal computer; DAC—digital-to-analog converter.

significance of tactile reception under low-illumination conditions is comparable to that of visual reception [7, 8]. Tactile reception in vertebrates, as a component of the somatovisceral system, has no specialized sensory organs. The sense of touch or tactile sensitivity spreads diffusely throughout the integument of the fish body and head.

Until very recently, the algorithm of the formation of tactile information at the receptor level in fish remained an almost unstudied area in sensory physiology. Most of electrophysiological studies were devoted primarily to chemical sensitivity in fish, while responses evoked by non-normalized mechanical stimuli were demonstrated as a phenomenon only. Responses of chemosensory structures to mechanical stimulation in the fish skin were recorded in trigeminal and facial nerve fibers, as well as in the nuclei of corresponding projection areas of the brain [9–11]. The lack of data on the sensitivity and other physiological characteristics of fish tactile sensitivity might be due, specifically, to a limited set of methods allowing adequate stimulation in a dose-dependent manner. The aims of this work included (1) recording and evaluating the parameters of electric responses in the fish skin to normalized tactile stimulation, (2) determining the threshold value of a tactile stimulus, (3) identifying specific types of cutaneous tactile receptors, (4) analyzing the distribution of tactile sensitivity over the fish head.

MATERIALS AND METHODS

A total of 12 individuals of the silver crucian carp *Carassius auratus gibelio* (length, 9–12 cm) and 5 common carps *Cyprinus carpio* (length, 12–15 cm) were used in experiments. Experimental fish were kept in a 50-L aquarium and fed with mosquito (chironomid) larvae supplemented with dry feed. Before the experiment, the fish was immobilized in a plastic box (27 × 9 × 5 cm) in such a way that all its body was submerged in water except for the area on its head intended for testing.

Recording of receptor potentials requires a clean skin free of scales. For this reason, tactile sensitivity was recorded on the fish head only. The gills of the experimental fish were constantly perfused with water at 18–19°C. Fish immobilization was provided by a high velocity of flowing water (150 mL/min). Myorelaxants were not used. After completion of the study, fish released to an aquarium carried on swimming and feeding, being apt for further experimental use.

To measure tactile sensitivity, we used a previously approbated technique of noninvasive recording of electric potentials on the surface of the fish head [12, 13]. This method allowed sequential (within the same experiment) testing of skin areas on the dorsal, lateral and ventral sides of the head without damaging the skin surface.
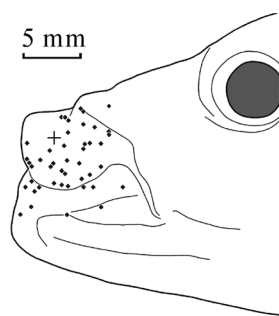
Fig. 2. Schematic representation of data from a single experiment on testing the lateral perioral area of the crucian carp, *Carassius auratus gibelio*. The position of the recording electrode is indicated by a cross. The points on the skin, tactile stimulation of which evoked responses, are shown with diamond marks.

Tactile stimulation was carried out by resilient nylon monofilaments (MF), 30–50 mm long, bent in their terminal part. Each MF had a pre-melted end face in the form of a small sphere 1 mm in diameter. MFs were fixed in a clamp of the electromagnetic setup (tactile stimulator, Fig. 1) which under the control of signals from a digital-to-analog converter (DAC) sequentially, four times per single recording, directed MF towards a test area on the fish skin. The stimulation cycle of four stimuli is shown in Fig. 1. The duration of leading edges of setup triggering during stimulation was 4 ms, the delay time of the onset of MF movement relative to the leading edge of the control pulse did not exceed 1 ms.

Overall, it was used six types of MFs of different rigidity. The force applied to the skin surface during stimulation by the end face of the most soft MF was 0.04 g, that of the most rigid MF was 1.3 g. Considering the contact area of the spherical MF end face equal to 0.8 mm^2, the pressure that corresponded to these forces at the contact area was 0.05 and 1.6 g/mm^2, respectively. MFs that provided intermediate stages of the stimulatory force were adjusted in such a way that, while transiting to the next stage towards increasing, the pressure on the skin surface would rise twofold (0.08, 0.16, 0.32, 0.64 g). The force developed by each MF sample upon triggering the stimulation setup was calibrated using a balance HL-100 (A&D, Japan). When preparing for experiments, the force developed by MFs was regulated by selecting the MF diameter (rough selection) and

changing its length (precise selection).

A chloro-siver wire, 0.3 mm in diameter, enclosed in a glass capillary was used as a recording electrode. The space between the electrode and in inner capillary wall was filled with water from the aquarium. A fritted capillary end face tightly, without gaps, adjoined the skin surface. Signal from the electrode was fed to the input of a DC amplifier with an input resistance of 1 GΩ, frequency band up to 2 kHz, and zero auto-compensation system activated by the program in interrecording intervals. An amplified signal was transmitted to one of the inputs of an analog-to-digital converter (ADC E14-440; L-Card, Russia). Simultaneously, a control signal of the electromagnetic setup for MF feeding was recorded through the other ADC channel. After converting into a digital code with a 20 kHz sampling rate, these data were stored in computer memory. ADC operated under control of the Lgraph II software (L-Card, Russia).

The MF movement cycle sequence was determined programmatically. Each recording lasted 5.8 s and included the background activity interval (1.8 s before the onset of stimulation), responses to a fourfold mechanical stimulation of the skin area under study (1.4 s), and electric potential variations in the aftereffect (2.6 s). During the initial search for skin sites, mechanical stimulation of which evoked an electric response, we used MF that created a force of 1.3 g while pressing. The interval between the sequential stimulation cycles was no less than 8 s.

Before the onset of stimulation, the MF end face touched the skin site under study without pressing. Mutual location of the electric stimulation points depended on anatomy of the head area of our interest. For example, when testing the lip sensitivity, the electrode was installed on the upper or lower lip, and then the lips themselves and the adjacent skin areas were stimulated. When studying the other areas, the electrode end face was positioned most frequently within the area to be studied (Fig. 2).

To visualize test areas on the fish head, a video camera CNB-ZBN-21Z27F (CNB, China) was used. Stimulation points were fixed in a polar coordinate system relative to the sites where the end face of recording electrode adjoined the head

skin. The distance between the electrode end face and tactile stimulation points varied from 1 to 15 mm.

To test tactile sensitivity at each skin site of interest, we measured a threshold force of mechanical pressure on the skin surface which evoked a deflection of the recorded potential from the baseline by at least 0.1 mV.

The response threshold was determined in the interval between two stimulus values provided that a higher-amplitude stimulus evoked a response while a lower-amplitude stimulus did not.

Polarity of electric responses was considered straight at a positive potential shift in response to an increase in the MF pressure on the skin. If an increasing mechanical pressure led to a potential deflection towards negative values, such a response was called inverse. While decreasing the MF pressure on the skin, the "straight" response looked as a potential deflection towards negative values, whereas the "inverse" response changed towards positive values.

Overall, 32 experiments were carried out, including a total of 2500 recordings. Of this number, responses to tactile stimulation were detected in 1200 cases.

More than a half of the total number of recordings (1300) displayed no signs of a response to stimulation. This group included control potential recordings during MF movement near the fish head (without touching the skin) or results of stimulation of touch-insensitive or low-sensitive skin sites.

During data analysis, the experimental probability (p_e) of responses generated to stimulation within the test skin site was calculated as a ratio of the number of recorded responses to the number of stimulus presentations. The latency and the duration of the rising phase (rise time) of responses to tactile stimulation were measured after experiments using the SoundForge 10 Pro software (Sony, Japan). The level 0.1 from the response maximum was considered a moment of the response onset; accordingly, the moment of the response decay was counted from the level 0.9 relative to the preceding response maximum.

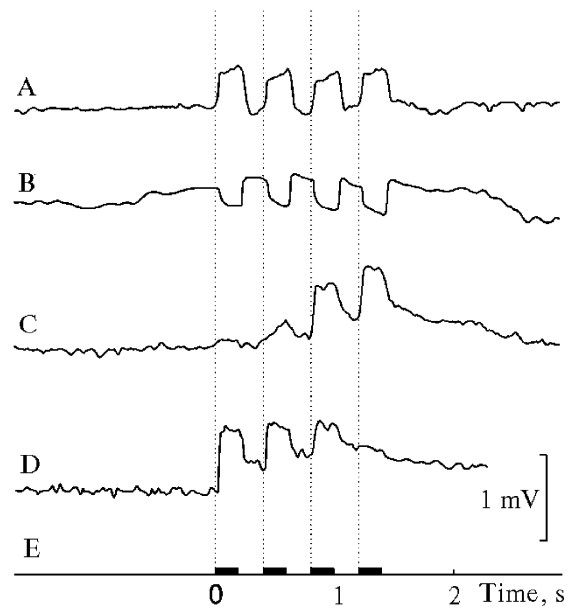To confirm that the recorded responses originated from tactile receptors, we ran a series of six

Fig. 3. Tonic (DC) responses to quadruple alternating tactile stimulation of the crucian carp (*Carassius auratus gibelio*) upper lip. A—straight response (middle part of the lip); B—inverse response (middle part of the lip); C—summation of the sustained component of the response with a gradually increasing alternating component (lateral part of the lip); D—the same, but with a decreasing alternating component; E—sequence of stimulating episodes: black bars indicate the individual tactile stimuli, each of 0.2 s in duration.

control experiments with lidocaine, a voltage-dependent sodium channel blocker [14], which was applied either topically using a small cotton tampon soaked with 2.0% lidocaine solution or through a subcutaneous injection of 20 µL of lidocaine solution to the test area of the head. Activity of tactile receptors was recorded before lidocaine application and repeatedly 4−5 min thereafter. Then, during the next 20 min, the dynamics of changes in the parameters of electric responses was tracked in response to tactile stimulation until the response amplitude reverted to the initial level.

RESULTS

Electric responses to tactile stimulation

During experiments, there were recorded three types of responses: tonic (DC) responses in the form of potential fluctuations repeating the dynamics of a quadruple stimulus (Figs. 3A, 3B), phasic (AC) responses as on-, off- and on-off
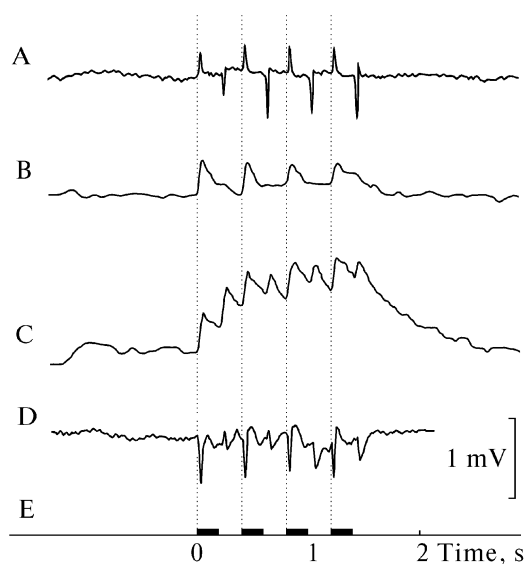
Fig. 4. Examples of phasic (AC) responses to tactile stimulation of the ventral side of a crucian carp (*Carassius auratus gibelio*) head. A—on-off responses; B—on-responses only to the moments of pressure increase, with some signs of summation with the tonic (DC) component of the response at the fourth stimulus level; C—unipolar on- and off-responses summed with slowly rising sustained response potential; D—negative on-responses combined with increasing off-responses (to the moments of pressure relief); E—stimulation, see Fig. 3.

potentials (Figs. 4A, 4B, 4C), and slow potentials with a total duration exceeding the total time of the stimulation cycle. There were also recorded complex responses combining reactions of tonic and phasic receptors with slow potentials (Figs. 3C, 3D, 4C). The recording probability of tonic and phasic receptors was similar (44 and 37%, respectively). The fraction of slow responses accounted for 19% of the total number of responses. The polarity of tonic and phasic responses could be both straight and inverse (Figs. 3A, 3B) relative to the MF pressing cycles during stimulation.

In tonic responses, the amplitude of potentials that followed synchronously with stimulation cycles was most often constant, but in some experiments, there were observed both a gradual increase (Fig. 3C) and a smooth decline (Fig. 3D) in the response amplitude.

Phasic responses were observed in several forms and combinations of different types: surges of the receptor potential to an increase and subsequent pressure reliefs (Fig. 4A); responses only to leading edges of tactile stimuli, sometimes with signs of summation with a tonic component (Fig. 4B); unidirectional positive responses to all leading edges of mechanical stimulus switching independently of the stimulus direction, and those combined with a slow potential (Fig. 4C); negative phasic responses to rising and falling edges of the pressure force (Fig. 4D).

By analogy with the processes accompanying tonic responses, the amplitude of the short potentials in phasic responses could change (increase or decrease) during stimulation. Multiple stimulation of a single touch-sensitive point by identical dosed stimuli, as a rule, led to a decrease in the response amplitude and a falling-out of some of its components.

Particularly strong tonic and phasic responses arose to a sliding movement of the MF end face along the skin surface. However, this feature can be noted as a phenomenon only, since it was impossible to normalize physical parameters of such a stimulation under conditions of the applied technique.

Latency of electric responses to tactile stimulation

The latent period of the rising edge of tonic responses relative to stimuli averaged 6.1 ms (root-mean-square deviation $\sigma = 3.3$ ms); accordingly, the falling edge delay was 9.8 ms ($\sigma = 6.0$ ms). No dependence between the value of the latent period and the number of an individual stimulus in a quadruple sequence was detected. The latent period of responses of phasic receptors to leading edges of stimuli averaged 4.4 ms ($\sigma = 2.7$ ms), while to trailing edges 4.1 ms ($\sigma = 3.1$ ms).

Effect of lidocaine on tactile responses

Lidocaine application to the surface of the test skin site by a cotton tampon or subcutaneous lidocaine injection evoked a similar pattern of changes in electric responses to tactile stimulation in all six experiments of the given series. The amplitude of recorded responses increased several times ($p = 0.95$ by Wilcoxon T-test) 2–3 min after lidocaine application (Fig. 5). Increased excitability in response to tactile stimulation persisted during about 10 min. After that, the amplitude

gradually declined during roughly the same time interval to the level that was several times lower than the initial, and then recovered up to the initial level over 2–3 min.

Zonal distribution of tactile sensitivity over the fish head surface

An analysis of the distribution of tactile sensitivity over the head surface allowed distinguishing several sensory areas which responded to tactile stimulation: on the lateral side of the head—perioral, nasal and orbital (Fig. 6A), on the dorsal side—perioral, nasal and interorbital (Fig. 6B), and on the ventral side—perioral, gular and interbranchial (Fig. 6C). These areas were different by the level of sensitivity to tactile stimulation and the response probability in testing adjacent skin sites. Each sensory area of the head skin exhibited its specific combination of tonic, phasic and slow responses to tactile stimulation.

A high tactile sensitivity and a high probability of responses ($p_e = 0.84$) characterized the perioral areas which cover the upper and lower lips and the perilabial skin areas (Fig. 2; Fig. 6, area *1* at each of the sides). In the perioral area in the lateral part of the upper lip, there were recorded phasic and tonic responses only. In the perioral area on the dorsal head surface in the central part of the upper lip, there were recorded predominantly slow potentials, as well as tonic responses. Tactile stimulation of the upper lip sometimes evoked the motor reaction of the body and tail. The skin near the upper lip also exhibited a high tactile sensitivity, responding to tactile stimuli of 0.04 g (0.05 g/mm^2) in the form of tonic responses or slow potential fluctuations.

The intercontacting lateral areas of the lower and upper lips were characterized by particularly low thresholds of tactile sensitivity. Here, there were recorded responses to a pressure of 0.05 g/mm^2. On the ventral side of the head, in the skin areas located near and caudally to the upper lip, there was also detected a high tactile sensitivity manifested as tonic and phasic responses.

The distribution of different types of responses in the perioral areas (Fig. 6, area *2*) on the lateral, dorsal and ventral sides of the head was similar. In these areas, tonic and phasic responses occurred at an almost equal proportion, accounting for 36–
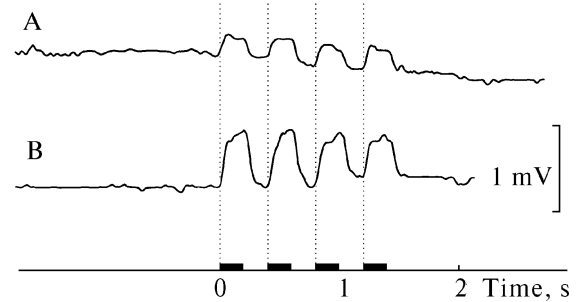

Fig. 5. A lidocaine-induced increase in the amplitude of tactile responses in the test area of the carp (*Cyprinus carpio*) head. A—before lidocaine application; B—5 min after lidocaine application. The area of tactile stimulation and electrode position are the same as in Fig. 2. For other designations see Fig. 3.

41%. There were also recorded compound (phasic-tonic) responses, as well as responses combined with slow potential fluctuations. The slow type of response was observed mainly on the dorsal side of the head, both in the parioral (23%) and nasal (18%) areas. On the lateral and ventral sides in the perioral areas, the slow response type manifested itself just in 10% of recordings. In the nasal area on the lateral side of the head, the ratio of tonic and phasic responses was similar to that in the perioral areas: 46% of tonic and 36% of phasic responses.

On the lateral side of the head, the nasal and orbital areas (Fig. 6A, areas *2, 3*) were far less sensitive to tactile stimuli compared to the perioral areas (Fig. 6A, area *1*). For example, in the nasal and orbital areas on the dorsal side of the head, threshold responses in the form of stimulus-synchronized potential shifts with an amplitude of more than 0.1 mV arose in the pressure range of 0.2–1.6 g/mm^2, while in the perioral areas responses were recorded at a pressure varying from 0.05 to 0.2 g/mm^2. In the nasal area on the dorsal side of the head (Fig. 6B, area *2*), tactile responses were only recorded at an even higher pressure—no less than 1.6 g/mm^2. In the interorbital area on the dorsal side of the head (Fig. 6B, area *3*), tactile responses were not detected.

On the ventral side of the head, caudally to the perioral area, the central position is occupied by the gular area (Fig. 6C, area *2*). The rostral part of this area was characterized by a particularly high
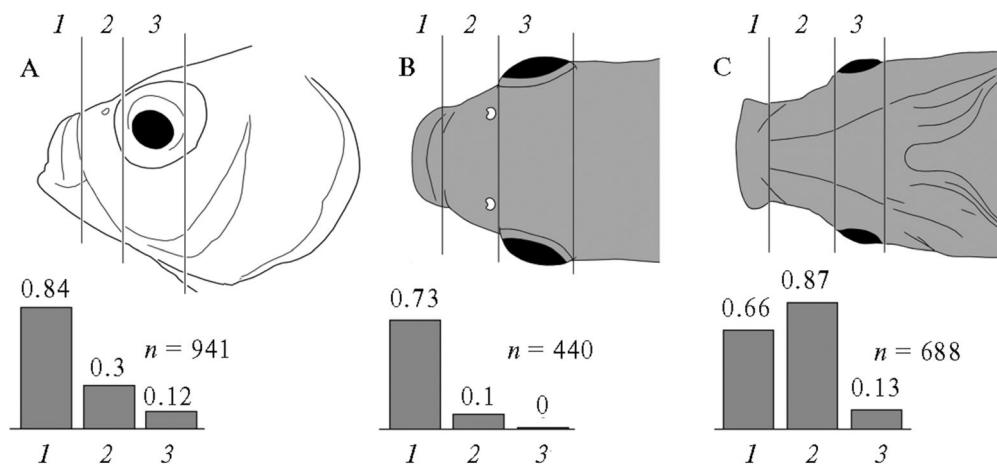
Fig. 6. Sensory areas on the fish head (*Carassius auratus gibelio*), where tactile reception was studied. A—on the lateral side: perioral (*1*), nasal (*2*), orbital (*3*); B—on the dorsal side: perioral (*1*), nasal (*2*), interorbital (*3*); C—on the ventral side: perioral (*1*), gular (*2*), interbranchial (*3*). Bar charts in the insets for each side show the probability of responses (p_e) in each area. Numbers near the bar charts stand for the total number of tactile stimulation tests presented to each side.

probability of responses to tactile stimulation ($p_e = 0.87$). In this area, the adjacent points on the skin surface differed from each other in their threshold sensitivity by 1–2 gradations. As judged from the intensity of responses to minimum tactile stimulation, sensitivity thresholds at some points of this area were lower than the minimum level of the tactile stimulus (0.04 g; 0.05 g/mm^2).

In the central part of the gular area, there were observed the signs of co-activation of tonic and phasic receptors. In contrast to the orbital areas on the dorsal and lateral sides, in the gular area phasic responses prevailed. At different points of the gular area, responses differed not only by their type but also by the amplitude and duration. In the rostral part of the gular area, there occurred the sites yielding only phasic and sometimes on-off responses. In the caudal part of the gular area, tonic responses (51%) were recorded more frequently compared to phasic (39%).

On the surface of most lateral parts of the gular area, the probability of tactile responses ($p_e = 0.3$) was almost thrice as low as in its central part ($p_e = 0.87$). Response thresholds in these area also proved to be 2–4 times higher compared to the central part of the gular area. In the skin of the interbranchial area (Fig. 6C, area *3*), the probability of tactile responses was low ($p_e = 0.13$).

Thus, the distribution pattern of the tactile system's parameters on the surface of the fish head (silver crucian carp, common carp) demonstrates a trend towards decreasing the sensitivity level and the probability of electric responses to mechanical stimulation in the rostrocaudal and ventrodorsal direction.

DISCUSSION

When analyzing the obtained data, it was important to solve the issue of the origin of recorded potentials. Two factors indicate that activity of tonic and phasic receptors recorded in our experiments reflect the primary electric processes (i.e. receptor potentials) in cutaneous receptors arising in response to mechanical stimulation: (1) small response delays (on average 6.1 ms for tonic and 4.1 ms for phasic responses), and (2) the characteristic effect of lidocaine, a voltage-gated sodium channel blocker [14], on the amplitude of evoked potentials. An increase in the amplitude of evoked potentials under the effect of lidocaine means that the sources of these potentials reside distally, i.e. prior to afferent fibers, and that the potentials owe their origin to receptors. The effect of summation of phasic and tonic responses, as recorded in our experiments, may be due to a high distribution density of different types of tactile receptors at certain skin sites of the fish head. This

is further confirmed by morphological studies which report an exceedingly high distribution density of nerve endings in superficial tegumental layers and especially in sensory areas of perioral and ventral localization [15−17].

The above features of skin innervation in fish can be considered as a basis for the diversity of types of responses to tactile stimulation recorded in this work. This diversity is characteristic of different types of mechanosensitive cells [18]. Responses to a mechanical pressure increase or a pressure relief reflect the activity of at least two subtypes (on- and off-) in each group of tonic and phasic receptors. Receptor complexes that respond antiphasically to a mechanical stimulus are long known in the lateral line system of fish and amphibians [19, 20]. It appears that such analogies in the functional repertoire of the mechanoreceptor systems reflect common principles of processing tactile sensory information in different vertebrate species.

Our experiments demonstrated that most intense tactile responses in all sensory areas of the fish head are evoked by sliding stimuli. Such a stimulus appears to be most adequate to signal the patterns of fish locomotion and orientation in the aqueous medium. The main flow of tactile stimulation on the fish head surface during swimming results directly both from external impacts and locomotion of fish themselves. Efficient processing of external information is possible provided that the two conditions are observed: (1) the sensory channel receives information about the motor program of animal locomotion, a so-called motor copy [21], and (2) the position of the dynamic range of receptor elements undergoes compensatory stabilization in accordance with the animal's motor activity [22]. The fulfillment of both conditions implies an active involvement of efferent regulation both in central divisions of the sensory channel and directly at the receptor level. It is this influence that may account for the diverse forms of temporal modulation of tactile responses, as well as response modification during repeated sessions of stimulating the same points on the head skin. The same factor may also explain a transitory increase in the amplitude of responses to tactile stimulation under the effect of lidocaine. We assume that lidocaine blocked the conduction of spike activity along efferent fibers and thereby promoted a decrease in the central inhibitory influence on tactile receptors.

A theoretical investigation of the processes of external signal extraction at the background of sensory flow evoked by the animal's own body movement demonstrated that the detection efficiency of weak external tactile signals under such conditions appreciably depends on the mode of sensory information presentation at the output of the sensory apparatus. Specifically, reception not only of the initial signal itself but also its time derivatives promotes increased efficiency of signal source detection [21, 22]. This may account for the abundance of phasic tactile receptors with different temporal response characteristics that were recorded in the present work.

The distribution of tactile sensitivity on the fish head is not uniform but zonal. The localization of sensory areas is species-specific and relates to the biological peculiarities of the given species [6, 7]. In our experiments on a silver crucian carp and a common carp, a maximum tactile sensitivity was detected in the head tegument of the perioral and ventral localization, while a minimum tactile sensitivity was localized to the dorsal and caudal areas. Apparently, such a distribution pattern has quite a definite underlying reason. The objects of the present study are facultative benthophages. For inhabitants of benthic biotopes, receptors both of rostral and ventral localization are of particular importance for foraging.

Zonal organization of tactile sensitivity constitutes a basis for the formation of the tactile sensory system in which each zone is a component of the whole system. The pattern of distribution and innervation of tactile sensory zones on the fish head coincides with the zonality in the distribution of taste reception [6, 23]. An interaction of contact and distant sensory systems is the alpha and omega of multisensory orientation and formation of complex behaviors in animals, including fish. The representatives of the family Cyprinidae, the objects of the present study refer to, are distinguished by a particularly high multisensory level of behavioral adaptations [2, 3].

Thus, using a noninvasive technique of recording cutaneous responses to tactile stimulation, we demonstrated that fish, like all terrestrial animals,

have both phasic and tonic tactile receptors. A great functional significance of tactile reception is provided by its physiological features, namely a high sensitivity and a low latency of responses, as well as its interaction with other sensory systems—visual and taste [9−11, 15].

The distribution pattern of tactile sensitivity on the head of the fish species studied herein relates to the features of their feeding behavior. An increased distribution density of tactile receptors in sensory head areas of cyprinid fish creates optimal prerequisite for spatial orientation, as well as the search and recognition of food objects.

FUNDING

AUTHOR CONTRIBUTION

G.V. Devitsyna was responsible for the problem statement, designing the experiments, data collection, text writing and editing.

D.N. Lapshin was in charge of developing the experimental technique, data collection, text writing and editing.

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