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Experience of Pain and Fear in Fish from the Neurocognitive Perspective

Ощущение боли и страха у рыб с нейрокогнитивной точки зрения

Абстракт

Статья представляет собой обзор современного состояния исследований одного из аспектов чувствительности и внутренней жизни рыб, который еще редко принимается во внимание, то есть формирования болевых ощущений, аффективных состояний и эмоционального опыта. Для того чтобы сделать выводы о возможности испытывать эмоции рыбами, необходимо сначала ответить на вопросы о базовых аспектах, характеризующих когнитивные процессы у рыб: способны ли рыбы формировать специфические физиологические ощущения, такие как болевые ощущения (ноцицепция), и развиваются ли у рыб простые аффективные состояния, например страх или тревога, которые коррелируют с ощущением боли? Рудиментарный характер этих вопросов вытекает из предположения, что простейшие поведенческие реакции и когнитивные ощущения являются необходимым условием формирования более сложных познавательных структур, таких как сенсомоторные переживания, ментальные представления и эмоциональные состояния.

Experience of Pain and Fear in Fish from the Neurocognitive Perspective

Abstract

The article is an outline of the current state of knowledge about the aspect of the sentience and internal life of fish, which is still too rarely taken into account – about the construction of pain experiences, affective states, and possible emotional experiences. In order to draw conclusions about the possibility of fish feeling emotions, firstly it is necessary to answer questions about simpler content that characterize the fish cognitive system: whether fish are able to create a special type of affective-physiological experience, such as pain with distress, and whether fish have simple affective states – fear or anxiety – which are correlated with the experience of pain. The rudimentary nature of these issues results from the assumption that the simplest behavioural reactions and cognitive-affective sensations are considered a necessary condition for the ability to construct more complex cognitive structures, such as sensorimotor experiences, mental representations and emotional states. The ability to experience pain and the correlated ability to feel negative affect, such as fear or anxiety, can be considered indicators of a species' possession not

Способность ощущать боль и связанная с ней способность испытывать негативные аффективные состояния, такие как страх или тревога, могут рассматриваться как показатели наличия у вида не только физиологических потребностей, но и психических предпочтений. Таким образом, способность ощущать боль, страх и тревогу можно считать предиктором когнитивно-поведенческой гибкости и когнитивного контроля у рыб.

Ключевые слова: боль у рыб, страх у рыб, тревога у рыб, эмоции рыб, познание у рыб, сознание рыб, восприятие у рыб

only of physiological needs, but also of mental preferences. Thus, the ability to experience pain with fear and anxiety can be treated as a predictor of cognitive-behavioural flexibility and a certain degree of cognitive control in fish.

Keywords: fish pain, fish fear, fish anxiety, fish emotions, fish cognition, fish awareness, fish perception

Introduction

For cognitive neuroscience, fish are a particularly interesting group of vertebrates due to their specific cognitive adaptation to the underwater ecosystem. At the same time, fish belong to a taxon within which they differ so much in their structural features that taxonomists suggest fish should be considered a superclass corresponding to Tetrapoda and divided into classes equal to reptiles, birds, or mammals. Although the majority of contemporary fish belongs to Osteichthyans, yet the main feature of their cognitive system, common also to Chondrichthyes, is having specialized receptors of chemical, balance, and mechanical senses. As Jonathan Balcombe argued in his excellent book *What a Fish Knows*, the cognitive system of probably all fish constructs experiences, simple representations and mental processes that manifest in such highly intelligent activities as "planning, tool use, courtship parties,"[1] as well as through "interspecific communicative and coordinated hunting between individuals of the two species."[2] In order to reach the very foundations of the construction of mental representations and experiences by fish, and also due to certain ethical and legal consequences, I am going to be interested here in the more fundamental process of creating simple, but polymodal interoceptive-affective experiences. As we will see later in the text, the extraordinary sensitivity of fish receptors to mechanical, thermal and chemical environmental changes is one of the evidences that fish feel intense, polymodal pain experiences – especially when fish

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[1] Jonathan Balcombe, *What a Fish Knows?* (New York: Scientific American / Farrar, Straus & Giroux, 2016), 241.

[2] Redouan Bshary et al., "Interspecific Communicative and Coordinated Hunting between Groupers and Giant Moray Eels in the Red Sea," *PLoS Biology* 4, no. 12 (2006): e431.

become the subject of breeding, transport, and slaughter. Another discussed proof of the advanced perception of pain in fish is the fact fish have an extensive network of nociceptors and the structure of neural pathways, whose tiered architecture implies they play a role in consolidation of complex experiences of affective and pain nature. Being aware of all those scientific arguments it should be said that fish need to be granted the moral status and an effective legal protection as subjects of experience, namely, organisms of high sensitivity or sentience to all harmful factors and aversive stimuli.

Concerning formal aspects, the text is divided into three problem sections: the first one describes fish capacity to sense simple pain sensations (nociception) and to feel complex pain experiences (pain perception). The second section discusses fish ability to construct affective experiences, with particular emphasis on fear. The third, shortest section, emphasizes the broad topic of hormonal indicators of pain and fear in fish, such as stress hormones. Discussing the behavioural evidence for the experience of negative emotions in fish (e.g. behaviour in fish) would extend the length of this article too much, so the behavioural evidence is omitted. The whole discussion ends with conclusions. Whenever fish are mentioned in this text, "fish" should be understood as the entire infraclass of *Teleostei*, representing the largest infraclass in the ray-finned fishes class. Whereas, whenever experiencing of the phenomenon of pain is discussed, in each case it is understood according to the definition proposed by the International Association for the Study of Pain (IASP), where pain is defined as "an unpleasant sensory and emotional experience associated with, or resembling that associated with, actual or potential tissue damage."[3] In accordance with the said definition, the phenomenon of pain is not a simple sensation, but a complex experience, representing integrated sensory sensations.[4]

Pain Sensation and Pain Experience in Fish

Nociception is understood as a physiological ability to detect aversive changes in tissues by specialist receptors located in the epidermis or dermis, and then process those changes in the spinal cord or paired ganglia joined by connectives.[5] In other words, this process means registering of physical – mechanical, thermal or

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[3] Cf. https://www.iasp-pain.org/resources/terminology/.

[4] Edgar T. Walters and Amanda C. de C. Williams, "Evolution of Mechanisms and Behaviour Important for Pain," *Philosophical Transactions of the Royal Society B* 374, no. 1785 (2019): 20190275.

[5] Emer M. Garry et al., "Nociception in Vertebrates: Key Receptors Participating in Spinal Mechanisms of Chronic Pain in Animals," *Brain Research Reviews* 46 (2004): 217.

chemical – injuries in the tissue at the level of reception of an aversive proximal stimulus by nociceptors, which then synaptically transmit projections to the said spinal cord and further on, to higher cortical centres (somatosensory cortex, the frontal cingulate gyrus, and the insula), or functionally analogous neural structures in the selected groups of invertebrates. Processing of the nociceptive stimulus triggers a sensation, expressed in an automatic nocifensive reflex, that is, withdrawal of a part or of the entire body away from harmful changes in the environment.[6]

If we ask which taxa in the Animalia kingdom are able to implement nociception, the answer would be that in theory it is possible for all organisms that have a nervous system (not necessarily a centralized one) and nociceptors, that is, free nerve endings located in tissues. Therefore, all vertebrates and some invertebrates are at least capable of the act of nociception, namely, transforming harmful changes in the environment into sensations of pain, if not of a more complex perception of pain and generating polymodal pain experiences. Nociception results in a behavioural reaction, known as a nocifensive reflex, to aversive stimulations and changes. Therefore, if in specific circumstances an individual withdraws its body or limb away from a harmful stimulus, it possibly feels a simple sensation with negative (unpleasant) valence. This reflex was demonstrated already in Platyhelminthes having a distributed neurosensory network, and specifically in *Notoplana aticola*, a species of Polycladida. Those animals responded with a locomotor reaction of escape when a researcher pricked the posterior part of their body with a pin.[7] Although to this day no actual nociceptors were found in Turbellaria, yet their neurons react to mechanical stimuli in a way indicating that aversive sensations are generated. Neurons with the nociceptor function were identified in Annelida, specifically in the European medicinal leech (*Hirudo medicinalis*), in which every segment of the body contains a separate ganglion connected with receptors of the touch modality (haptic-tactile receptors), baroreceptors (sensing changes in the pressure) and nociceptors.[8] Nociceptors are also found in

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[6] David DeGrazia and Andrew Rowan, "Pain, Suffering, and Anxiety in Animals and Humans," *Theoretical Medicine and Bioethics* 12, no. 3 (1991): 195.

[7] Harold Koopowitz, "Primitive Nervous Systems. A Sensory Nerve-Net in the Polcald Flatworm *Notoplana acticola*," *The Biological Bulletin* 145 (1973): 352–359.

[8] John G. Nicholls and Denis A. Baylor, "Specific Modalities and Receptive Fields of Sensory Neurons in CNS of the Leech," *Journal of Neurophysiology* 31, no. 5 (1968): 740–756; Alan D. Workman et al., "Modeling Transformations of Neurodevelopmental Sequences Across Mammalian Species," *The Journal of Neuroscience* 33, no. 17 (2013): 7368–7383; Lynne U. Sneddon et al., "Do Fishes Have Nociceptors? Evidence for the Evolution of a Vertebrate Sensory System," *Proceedings of the Royal Society* B 270, no. 1520 (2003): 1115–1121; Lynne U. Sneddon, "Comparative Physiology of Nociception and Pain," *Physiology* (Bethesda, Md.) 33, no. 1 (2018): 63–73; Lynne U. Sneddon et al., "Defining and Assessing Pain in Animals," *Animal Behaviour* 97 (2014): 201–212.

Arthropoda, for example, in the common fruit fly (*Drosophila melanogaster*), and in molluscs, among which nocifensive reflexes were studied, for example, in Cephalopoda and species of marine (*Tochuina gigantea* and *Aplysia californica*) or land (the brown-lipped snail, *Cepaea nemoralis*) snails.[9] For over fifty years, the nocifensive reflex has been considered as the behavioural evidence of feeling the simplest sensation of pain in the animal kingdom. A higher, that is, more complex experience of pain and emotions is an effect of a cognitive process of pain perception, as indirectly proven by patients with injured spinal cord, who have an automated reflex without aware experiencing pain. This is caused by the fact that the nocifensive reaction does not require afferent, neuronal impulsation, transmitted "above" the spinal cord, that is, processing of pain projections in the process of integration of sensations at the subcortical level (in the thalamus of the diencephalon). Nevertheless, the nocifensive reaction at the level of the spinal detection of stimuli appears to be a very simple and phylogenetically the oldest form of embodied, non-affective and automated assessment of external stimulations as either positive or negative.

When we analyze the neural architecture of pain in fish, for more than half a century researchers have known about the presence of free nerve endings in *Teleostei* bodies, and this indicates the presence of fully developed nociceptors. More specifically, in 1971 Mary Whitear described chemosensory and mechanosensory nerves in fish epidermis suggesting that they might be related to the sensation of pain.[10] However, only after 2002 the precise structure of nociceptors was determined – with the rainbow trout (*Oncorhynchus mykiss*) as the example – as free, completely naked nerve ends, by using electrophysiological and neuroanatomical methods.[11] The structure of the nociceptive system in fish is a part of a more extensive somatosensory system forming a network of nerves that registers and processes specific stimuli of tactile, thermal, kinestetic, and pain modalities. At the molecular level, nociception in fish involves ion channels generating cascades of thermal pain sensations when exposed to excessively high temperatures, while in species inhabiting tropical waters, nociceptors reacting to cold were discovered. In fish,

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[9] See: Vincent Castellucci and Eric R. Kandel, "Neuronal Mechanisms of Habituation and Dishabituation of the Gill-Withdrawal Reflex in Aplysia," *Science* 167 (1970): 1745–1748; Paul A. Illich and Edgar T. Walters, "Mechanosensory Neurons Innervating *Aplysia siphon* Encode Noxious Stimuli and Display Nociceptive Sensitization," *Journal of Neuroscience* 17, no. 1 (1997): 459–469.

[10] Mary Whitear, "The Free Nerve Endings in Fish Epidermis," *Journal of Zoology* 163 (1971): 231–236.

[11] Paul J. Ashley et al., "Nociception in Fish: Stimulus-Response Properties of Receptors on the Head of Trout *Oncorhynchus mykiss*," *Brain Research* 1166 (2007): 47–54; Lynne U. Sneddon, "Anatomical and Electrophysiological Analysis of the Trigeminal Nerve in a Teleost Fish, *Oncorhynchus mykiss*," *Neuroscience Letter* 319, no. 3 (2002): 167–171; Christopher J. Tayloret et al., "A Novel Zebrafish-based Model of Nociception," *Physiology & Behavior* 174 (2017): 83–88.

the endogenous opioid system, involved in prevention of the pain feelings, is also very similar to that found in mammals.[12]

The perception of pain is a process of higher complexity of stimulation processing than nociception; where in the latter only simple bodily reflexes are elucidated in response to a monomodal aversive sensations. The perception of pain means a polymodal – physiological, sensory, and affective – experiencing of harmful changes in own tissues. Thus, it is an ability to generate negative, complex cognitive experiences of an emotional character in the form of bundles of affects and pain sensations as well as anticipative simulations (predictions) of possible experiences on the basis of associations and sensory-affective representations. They are remembered for a long time and endogenously initiate top-down preventive and defensive actions. Stimulations acting on nociceptors can simultaneously trigger action potentials in tactile receptors, which complement impulsation of nociceptive stimuli with parallel projections along pathways for processing of harmful thermal, chemical, and mechanical changes.[13] In fish, the organ able to receive too intense mechanical pressures with simultaneous generation of pain experiences is the lateral line with its accompanying nervous pathways, and I am going to discuss it further below. Concerning processing of proximal stimuli in cortical structures, pain nocicepts are integrated with intense haptic-tactile sensations, while neurocircuits of affective reactions supplement the sensory experience with an emotional reaction of fear and a physiological reaction of stress.[14] This polymodal stimulation results in the comprehensive percepts of pain as the experience of mental and physical suffering. If we were to propose a model mechanism for hierarchic generation of pain perception in fish, it would cover the following four stages:

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[12] Janicke Nordgreen et al., “Thermonociception in Fish: Effects of Two Different Doses of Morphine on Thermal Threshold and Post-Test Behaviour in Goldfish (*Carassius auratus*),” *Applied Animal Behaviour Science* 119, nos. 1–2 (2009): 101–107; Javier Lopez-Luna et al., “Impact of Analgesic Drugs on the Behavioural Responses of Larval Zebrafish to Potentially Noxious Temperatures,” *Applied Animal Behaviour Science* 188 (2017): 97–105; Nathalie Newby et al., “Morphine Uptake, Disposition, and Analgesic Efficacy in the Common Goldfish (*Carassius auratus*),” *Canadian Journal of Zoology* 87, no. 5 (2009): 388–399.

[13] Victoria A. Braithwaite and Philip Boulcott, “Pain Perception, Aversion and Fear in Fish,” *Diseases of Aquatic Organisms* 75, no. 2 (2007): 131–138; Fabiano V. Costa et al., “Understanding Nociception-Related Phenotypes in Adult Zebrafish: Behavioral and Pharmacological Characterization Using a New Acetic Acid Model,” *Behavioural Brain Research* 359 (2019): 570–578; Lynne U. Sneddon, “The Evidence for Pain in Fish: The Use of Morphine as an Analgesic,” *Applied Animal Behaviour Science* 83, no. 2 (2003): 153–162; Lynne U. Sneddon, “Trigeminal Somatosensory Innervation of the Head of a Teleost Fish with Particular Reference to Nociception,” *Brain Research* 972, nos. 1–2 (2003): 44–52.

[14] Joseph E. LeDoux, *The Emotional Brain. The Mysterious Underpinnings of Emotional Life* (New York: Simon & Schuster, 1996).

(1) reception and transduction of harmful stimulations in receptor cells, that is, the stage of sensory reception of proximal stimuli, changes, and stimulations in specialized sensory organs;

(2) transmission of tactile-haptic proximal stimuli and, simultaneously, nociceptive projections, which in fish is conducted through myelinated A-delta fibres and unmyelinated C-type fibres, and then through the spinal cord to the central nervous system; it is a stage at which detection and interpretation of features on the basis of the sensory memory occurs;

(3) subcortical integration of the signals as features of stimuli in the diencephalon (the thalamus), generating aversive tactile-haptic sensations and pain sensations (nocicepts), with simultaneous impulsation in circuits and modules of neural emotional systems;

(4) cortical integration of cascades of (thermal, chemical, mechanical, and nociceptive) sensations into multimodal experiences of pain in primary cortical fields and the working memory, with efferent physiological (stress), affective, and behavioural reactions. The behavioural reaction can be accompanied by mental conceptualization and categorization of sensory-affective suffering in the frontal lobe, and synchronous integration of long-lasting memory units as conditioned fear in different parts of the cortex. Here, I need to forestall the argument that fish do not have the neocortex. Neuroanatomists Jon Kaas and Glenn Northcutt, among others, demonstrated that the brain structure of lower vertebrates (including fish) contains areas having functions analogous to the mammalian neocortex,[15] though they are located in a different cerebral region.

Similarly to land mammals, Osteichthyans not only have free nerve endings, but also – initially discovered in the trout – two types of nerves transmitting pain stimuli: C-type unmyelinated fibres transmitting dull or pressing pain, and type A-delta myelinated fibres, quickly transmitting stabbing pain.[16] On this basis, the researchers finally characterized three types of nociceptors in Osteichthyans: polymodal, mechanothermal, and mechanochemical, which detect mechanical, chemical, and thermal injuries to the body, or their combinations. The intensity of the pain stimulus strength is coded by the frequency of action-potential discharges in the stimulated nociceptor – a more intense, for instance, pressure, prick, or impact results in a higher receptor potential, and this, in turn, elicits higher action potentials in A-delta myelinated and C-type unmyelinated fibres. At the same time, stronger pain

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[15] Glenn R. Northcutt and Jon H. Kaas, "The Emergence and Evolution of Mammalian Neocortex," *Trends in Neurosciences* 18, no. 9 (1995): 373–379.

[16] Ewan John Smith and Gary R. Lewin, "Nociceptors: A Phylogenetic View," *Journal of Comparative Physiology A. Neuroethology, Sensory, Neural, and Behavioral Physiology* 195, no. 12 (2009): 1089–1106.

stimuli activate a higher number of nociceptors, and therefore, a higher number of nerves leading from a given receptor to the spinal cord, from which the signal is transmitted through the medulla oblongata to the diencephalon, where the impulses coding aversive characteristics of the proximal stimulus are integrated into sensations of pain. The electrophysical studies confirmed that fish nociceptors are physiologically identical to mammalian ones. The evidence was provided, among others, by experiments from 2005, in which the researchers stimulated neural reactions in goldfish and trout using mechanoceptive and nociceptive stimuli.[17] Then, activation of successive stages of neuronal projection, from the spinal cord, through the cerebellum, up to mesencephalon, was monitored. It turned out that in both fish species, different forms of piercing, scratching, or a spot increase in the body temperature caused a bottom-up activation of all regions of pain perception, in A-delta and C-type fibres alike. Additionally, they activated the highest tier regions of emotional affect processing in the fish brain, including in the telencephalon. This neurologically complex nociceptive pathway confirms that fish feel complex pain and emotional experiences, where sensory, cognitive, and affective aspects are consolidated into comprehensive percepts. Successive studies that empirically confirmed those hypotheses were analyzed by already mentioned Victoria A. Braithwaite in 2007. The pain percept is a psychophysical experience that initiates processes of learning and creating memory traces that are of traumatic quality, and in consequence, causes changes in behavioural patterns during and after an aversive event. So when an animal has neural pathways used to detect, process, and feel results of the pain stimulation, while additionally, painkillers prevent certain behavioural changes in animals, then we have a double proof confirming occurrence of complex pain experiences.

Another area requiring attention in this respect is the lateral line which can be perceived as a neural disposition to generate polymodal experiences with an aversive/negative valence. Anatomically, it is a collection of subcutaneous microcanals filled with fluid and lined with the epithelium, with embedded groups of mechanoreceptors for detection of hydrodynamic changes, namely, changes in water pressure and movement.[18] Receptors of the lateral line are sensory bodies called canal neuromasts, where each sensory cell ends with a longer cilium (kinocilium)

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[17] Rebecca Dunlop and Peter Laming, "Mechanoreceptive and Nociceptive Responses in the Central Nervous System of Goldfish (*Carassius auratus*) and Trout (*Oncorhynchus mykiss*)," *The Journal of Pain* 6, no. 9 (2005): 561–568; Paul J. Ashley et al., "Effect of Noxious Stimulation upon Antipredator Responses and Dominance Status in Rainbow Trout," *Animal Behaviour* 77, no. 2 (2009): 403–410; Jessica J. Mettam et al., "The Efficacy of Three Types of Analgesic Drug in Reducing Pain in the Rainbow Trout, *Oncorhynchus mykiss*," *Applied Animal Behaviour Science* 133, no. 3 (2011): 265–274.

[18] Robert E. Shadwick and George V. Lauder, *Fish Physiology: Fish Biomechanics* (New York: Academic Press, 2006).

and a bundle of shorter cilia (stereocilia). The cilia react to the direction of water movement – stereocilia movement towards or away from the kinocilium results in an increase or decrease of cell membrane polarization, release of neurotransmitters, and generation of a neural signal through stimulated synapses. Neuromasts are connected to the central nervous system through branches of nerve pathways. Underwater vibrations and waves, flowing in through openings in the skin into the lateral line canals, exert a subtle pressure on neuromasts, which generate tactile sensations – it can be said that the fish is "touched" by flowing water. This way, it perceives the presence of other objects, passed organisms, or approaching or moving away from fixed items. All this is possible by registering reflected waves, caused by changes in water pressure, for example, when neighbouring fish in a shoal change their speed and direction.[19] The subtlety of the pressure of the flowing water results from the fact that the aquatic environment and the force of buoyancy acting on the fish eliminate a risk of possible mechanical damages to which land animals are exposed due to gravity. Therefore, the lateral line is adapted to much lighter pressure, and at the same time, is much more sensitive to tactile stimuli when compared to touch receptors in the skin of land animals. In consequence, the mechanical pressure on the lateral line – even under the weight of the fish's own body, especially when it lies on a rough surface – must be an extremely intense experience of pain, rarely felt by land mammals when they are pressed. Some of fish species have more than one lateral line, in some cases even up to five on one side of their body, as it is the case, for example, in the family Hexagrammidae belonging to the order Scorpaeniformes. In fish that do not have the lateral line, the tactile sensory receptors are much more numerous on their head.

Experience of Fear in Fish

As Barbara Finlay argues in her works, the brain of all vertebrates develops according to a common plan from the beginning of embryogenesis, although at different rates and with different results in different classes.[20] Yet we do not find anatomical structures in the vertebrate brain, which are precisely considered as the centre of emotional feelings, in fish and in Tetrapoda, including humans, there is a more or less developed limbic circuitry (including hypothalamus or bulbus olfactorius),

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[19] David H. Evans, *The Physiology of Fishes*, 2nd ed. (Boca Raton: CRC Press, 1998), 283–312.

[20] Christine Charvet et al., "Evo-Devo and Brain Scaling: Candidate Developmental Mechanisms for Variation and Constancy in Vertebrate Brain Evolution," *Brain Behavior and Evolution* 78, no. 3 (2011): 248–257.

integrating affective states.[21] Moreover, the different neuroanatomical structure of the fish telencephalon compared to the structure of the mammalian brain does not exclude the generation of simple emotional states. As it was already mentioned, Glenn Northcutt and Georg Striedter have repeatedly proven that in the brain of fish and amphibians there are areas functionally analogous or modules structurally homologous to functional modules and areas found in the neocortex of mammals.[22] "In fish the parts of the brain used during fear and pain responses are not anatomically the same (Broglio et al., 2003) as in mammals, but the function is very similar. […] Recent information about fear and pain behaviour (Portavella et al., 2004) shows that fish have in their brains areas with functions that closely parallel those of the amygdala and hippocampus in mammals."[23] Similarly, the system generating simple nocifensive reflexes and complex pain experiences is based on the same neurophysiology of nociceptors and nerve fibers in all vertebrates. For this reason, animal welfare researcher Donald Broom suggested over twenty years ago that we should abandon the artificial classification into different categories of pain and instead replace it with a uniform, sensory-affective system of pain in the animal kingdom.[24] On the other hand, other researchers recommend to differentiate between sensory pain as a specific class of sensations and sensory-affective suffering, perceived as complex experiences with a distinguishing component of fear. This classification enables empirical assessment of sensations and experiences together with different methods for alleviating different types of pain.[25]

We know that fish have neural modules capable of generating emotional states, so the question arises how the process of generating emotions in fish is carried out and what types of emotions fish are able to generate. Let us repeat for clarity: the evolution of the nervous system is a strongly conservative process; therefore, certain subsystems – advantageous for survival of entire taxa of animals – maintained their main structure and function, despite the phylogenetic development. In different groups of vertebrates there are close similarities in organization of their brain, and cognitive convergences. All vertebrates have the metencephalon, the mesencephalon, and the prosencephalon, which contain functionally the same neu-

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[21] Thomas Mueller, "The Everted Amygdala of Ray-Finned Fish: Zebrafish Makes a Case," *Brain, Behavior and Evolution* 97, no. 6 (2022): 321–335.

[22] Georg F. Striedter and Glenn R. Northcutt, *Brains Through Time: A Natural History of Vertebrates* (New York: Oxford University Press, 2020), 125–177.

[23] Manuel Portavella et al., "Avoidance Response in Goldfish: Emotional and Temporal Involvement of Medial and Lateral Telencephalic Pallium," *Journal of Neuroscience* 24, no. 9 (2004): 2335–2342; Donald M. Broom, "Fish Brains and Behaviour Indicate Capacity for Feeling Pain," *Animal Sentience* 3, no. 4 (2016): 2.

[24] Donald M. Broom, "Evolution of Pain," *Royal Society of Medicine International Congress Symposium Series* 246 (2001): 17–25.

[25] Adam Shriver, "Minding Mammals," *Philosophical Psychology* 19, no. 4 (2006): 433–442.

ral structures and anatomically the same nerve pathways in all vertebrates. Because "emotional systems in the brain are essentially the same in many of the backboned creatures, including mammals, reptiles, and birds, and possibly amphibians and fishes as well,"[26] researchers relatively quickly proved that fish not only have the nocifensive reflex, but they also experience complex, two-component pain percepts, that is, they feel negative physiological sensations with an addition of the aversive affective component – fear. How does this process of acquiring an additional affective component take place?

In subdisciplines of comparative psychology and affective neuroscience, there is an ongoing dispute whether non-human animals experience qualitatively the same emotional states as humans and whether these feelings can be called emotions at all.[27] On the one hand, there are arguments from supporters of the theory of primary affective systems[28] and psychoevolutionary theory of basic emotions,[29] according to which basic emotions require neither higher cortical structures nor higher-order thoughts to be experienced by mammals, and perhaps also "lower" vertebrates.[30] On the other hand, there are counter-arguments from supporters of the theory of constructed emotions,[31] who postulate that we should limit the use of concepts such as fear or joy only to conscious feelings occurring in humans and "higher" mammals (hominids, dolphins, rats, dogs, elephants, etc.). A reconstruction of the entire dispute is beyond the scope of this article. However, regardless of which of the debating sides has a more credible justification, it is possible to establish a compromise position that both defenders of basic emotions theory (Jaak Panksepp or Mark Solms) and supporters of the theory of constructed emotions (Joseph LeDoux, Lisa Barrett, James A. Russell) seem to agree on.

My compromise proposition I would call the "hypothesis of sensorimotor core affects," where analogous neuronal pathways and networks cause – in similar situations – (1) the same physiological arousal, (2) an equally positive or negative feeling of this arousal (valence), and (3) functionally identical behavioural patterns (avoidance, escape, freezing). My hypothesis refers to James Russell's idea that different

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[26] Joseph E. LeDoux, *The Emotional Brain. The Mysterious Underpinnings of Emotional Life* (New York: Simon & Schuster, 1996), 107; Joseph E. LeDoux, "Coming to Terms with Fear," *PNAS* 111, no. 8 (2014): 2871–2878.

[27] Lisa Feldman Barrett, *How Emotions Are Made* (Boston: Houghton Mifflin Harcourt, 2017).

[28] Jaak Panksepp, "Affective Neuroscience of the Emotional BrainMind: Evolutionary Perspectives," *Dialogues in Clinical Neuroscience* 12, no. 4 (2010): 533–545.

[29] Robert Plutchik, *Emotion: Theory, Research, and Experience*, Vol. 1 (New York: Academic Press, 1980).

[30] Jaak Panksepp, "The Basic Emotional Circuits of Mammalian Brains. Do Animals Have Affective Lives?," *Neuroscience and Biobehavioral Reviews* 35 (2011): 1795.

[31] Lisa Feldman Barrett et al., "The Experience of Emotion," *Annual Review of Psychology* 58, no. 1 (2007): 373–403.

emotional states have universal, underlying, neurophysiological attributes: a certain levels of arousal and valence.[32] I argue it is possible to outline an affective *continuum* of simpler sensations and more complex feelings, for example, fear, underlying increasingly complex neural modules, but activated by the same stimuli, mostly estimated as aversive. At one end of the *continuum* there is the experience of fear as a negatively valenced emotional episode, triggered by a physiological state (muscle tension, hormones), while at the other extreme would be the conscious feeling of fear, conceptualized and represented in a complex context of relationships and social norms. If emotional feelings require concepts that are available only to mammals, then other vertebrates, including fish and selected groups of invertebrates (Decapoda, arthropods, and mollusks) still have at least four simpler physiological-affective experiences: fear, rage, satisfaction, and perhaps the feeling of safety. The simplicity of these emotional episodes is that: (1) they do not require the participation of mental representations, such as the emotional feelings of shame, jealousy or pride,[33] but only sensorimotor associations, working memory and exogenous attention; (2) they arise from a combination of bottom-up physiological signals, kinesthetic and interoceptive sensations (e.g. hunger, muscle tension, increase in heart rate and temperature, pain sensations), secreted hormones and endogenously induced associations[34]; (3) these emotional experiences have only two characteristic features: high or low energy arousal and negative or positive valence and are a combination of the intensity of both features[35]; (4) although these are simple states, in relation to "higher" social feelings, they are still, somewhat paradoxically, sensory complex experiences. The complexity of such an emotion means that the subsequent behaviour (e.g. avoidance or defensive behaviour) is caused by long-term remembered, polymodal sensory associations of positive or negative valence. In other words, affective memory engrams have a multisensory aspect and are additionally subject to modifications under the influence of learning. Therefore, fear, rage or satisfaction in fish are not conceptualized feelings, but they are also not simple monomodal sensations. The idea of comparing simple affective states of animals to olfactory sensations was presented by Jonathan Birch, although his argument reduces affects to monomodal sensations, denying the complex structure of experience that I defend.[36] In my

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[32] James A. Russell, "Core Affect and the Psychological Construction of Emotion," *Psychol Rev* 110, no. 1 (2003): 145–172.

[33] Joseph E. LeDoux, *Anxious* (New York: Penguin Books, 2015), 42–43.

[34] Barrett, *How Emotions Are Made*, 56–57.

[35] James A. Russell, "A Circumplex Model of Affect: An Integrative Approach to Affective Neuroscience, Cognitive Development, and Psychopathology," *Development and Psychopathology* 17, no. 3 (2005): 715–734.

[36] Jonathan Birch, "Emotionless Animals? Constructionist Theories of Emotion Beyond the Human Case," *Proceedings of the Aristotelian Society* 124, no.1 (2024): 85.

opinion, the underlying emotional episodes in fish and other vertebrates are a subset of cognitive structures, experienced as polymodal percepts. Their feature is the body's motivation to react quickly, as well as flexible modifiability under the influence of learning (a stimulus that the fish was originally afraid of may be remembered as neutral); evaluating current stimuli and predicting phenomena in the environment and gradability, for example, from insecurity, through fear and anxiety, to panic, phobia or anxiety disorders.

So what is the difference between emotional experience and typically cognitive percepts? I will try to give the answer using the fear as an example. The affective state is characterized by an interoceptive quality and it has the function of positive or negative valence of the energy tension felt in the body by an animal (in the context of events and phenomena in the environment). So the first, main function of the experience of fear is to assess or evaluate changes (stimulations, stressors) that occur in the environment and in one's own body. "The core of the emotional system is a network that evaluates (computes) the biological significance of stimuli, including stimuli from the external or internal environment. The computation of stimulus significance takes place prior to and independent of conscious awareness."[37] Feeling somatic states of positive valence during changes in the body and the environment generates various degrees of arousal (eustress) as experiences of satisfaction – from calm relaxation to intense excitement. Likewise, feeling changes in the form of negative valence as distress has various degrees of energetic stimulation: from sadness and apathy, through fear and anxiety, to panic attacks. The second function of affective states in the animal kingdom is to create information (procedural and declarative knowledge) about the environment and one's own energy budget. The function of the emotion of fear would be an experience informing the animal about a potential or real threat, perceived or anticipated in the environment, as well as the experience of an expected threat resulting from energy deficits in its own body (e.g. as a result of existing or anticipated wounds, diseases, cold or hunger). The third function of emotions, especially fear, is to predict threats, anticipating unfavourable changes in the environment and one's own body, which should be prevented before they are fully realized.[38] In short, basic affective experiences – fear, anger, and satisfaction – can be defined as gradable physiological-sensorimotor states of positive or negative valence that are composed of simpler neural, endocrine and bodily components and perform universally basic cognitive functions. Due to the relatively simple mechanisms generating these affects, it is highly probable that they occur in lower vertebrates and some invertebrates, which has been repeatedly

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[37] Joseph E. LeDoux, "Cognitive-Emotional Interactions in the Brain," *Cognition and Emotion* 3, no. 4 (1989): 267.

[38] Barrett, *How Emotions Are Made*, 59–65.

confirmed experimentally. For example, as long-term research of Caroline and Robert Blanchards shows, the neuronal basis of fear and forms of its expression – withdrawal, immobility, defensive aggression, and submission – are similar in humans and other vertebrates.[39] The entire experience is caused by chemical, thermal, or mechanical injury to the body tissue. Here, affective states of discomfort, panic or fear are a crucial component, distinguishing pain as a complex experience from a simple reaction of the bodily evasion. Even though a roe deer runs away using its limbs, a bird flies away, and a fish swims away, coordinating different locomotor activities of their bodies, yet in these different locomotor patterns the internal motivation, the purpose, and the function of a motivation status and a behavioural pattern are the same: to separate the body from the hazard.[40] Therefore, the emotional status motivating the individual for locomotion will be the same across species: a certain form of fear, or, more general – a mobilizing feel of danger of an affective character.

The neurocognitive mechanism that conditions and structures the experience of fear in fish and other non-human vertebrates, in LeDoux's opinion, is a mechanism that (1) detects (adaptive) significance, or value of changes and stimulation and (2) triggers the appropriate sequence of behaviours.[41] The mechanism of conditioning the experience of fear or simply fear conditioning is a typical associative learning process in which the brain constructs long-term memories (engrams) with negative valence and high or low energetic arousal. During the conditioning, the nervous system processes stimuli (objects, phenomena, changes) and the accompanying negative physiological valence as an association, which becomes an interoceptive warning signal that danger is imminent. When similar stimulation or stressor occurs in the future, it elicits these associations, which then trigger fear-related responses (e.g., avoidance, freezing). So it is possible to consider an experience of fear as the interoceptive capacity to detect and respond to danger in animal kingdom, as LeDoux claims. "This ability is necessary to survive and is present in every animal, whether it's a worm, slug, crayfish, bug, fish, frog, snake, bird, rat, ape, or human."[42] Therefore, theoretically, if all vertebrates and invertebrates are capable of generating long-term experiences with negative valence (having for example the *corpus amygdaloideum* or analogous structure), then all these animals are predisposed to feel fear. From a neurocognitive perspective, the experience of fear in

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[39] See: Caroline D. Blanchard and Robert J. Blanchard, "Ethoexperimental Approaches to the Biology of Emotion," *Annual Review of Psycholology* 39 (1988): 43–68; Robert J. Blanchard and Caroline D. Blanchard, "Attack and Defense in Rodents as Ethoexperimental Models for the Study of Emotion," *Progress in Neuro-Psychopharmacology and Biological Psychiatry* 13, suppl. 1 (1989): S3–S14.

[40] Robert Plutchik, *Emotion: Theory, Research, and Experience* (New York: Academic Press, 1980): 3–33.

[41] Joseph E. LeDoux, *Anxious* (New York: Penguin Books, 2015), 24.

[42] LeDoux, *Anxious*, 42.

fish, other vertebrates and selected invertebrates is an interoceptive consequence of threat processing, as it is a cognitive state caused by an "interpretation of nonconscious ingredients generated by survival circuits."[43]

Hormonal Markers of Pain

Because pain experiences involve a negative affective component and represent a strong stressor, indicators of pain and negative valence in fish, that is, stress hormones, should be briefly discussed here. As researchers report, the most common factors inducing an integrated stress reaction in fish include extreme changes in their environment: water pollution, changes in the temperature, being caught on a hook or in a net, or taken out of water, but also longer interactions with humans, including practices used in the aquaculture, for instance, intense farming on the industrial scale, fishing, handling, and transport.[44] The stress reaction is a mechanism that is phylogenetically conservative; thus, despite different biotopes, the mechanism of the stress reaction in fish has many similarities with that of land vertebrates. Both in mammals and in fish, reactions to a stressor involve an immediate action of released catecholamines (e.g. adrenaline) and corticosteroids (e.g. cortisol). That last compound was identified less than fifty years ago in fish as the main stress hormone, released to the circulation from cells of the organ called pronephros, which function is analogous to that of the mammalian adrenal gland.[45]

Cortisol is an easily measurable component of negative emotional reactions and is of importance for fish welfare, as it influences brain physiology and functions, and modifies their behaviour. It can be used, with caution observed, as a practical indicator of affective-sensory states that will be experienced by fish in their environment.[46] Therefore, while cortisol secretion represents a response to a wide range of

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[43] LeDoux, *Anxious*, 28, 37.

[44] Natalie M. Sopinka et al., "Stress Indicators in Fish," *Fish Physiology* 35 (2016): 405–462; Elisabeth Urbinati et al., *Biology and Physiology of Freshwater Neotropical Fish* (London: Academic Press, 2020), 93–114.

[45] Sean Spagnoli et al., "Stress in Fish as Model Organisms," *Fish Physiology* 35 (2016): 541–564; Edward M. Donaldson, "The Pituitary-Interrenal Axis as an Indicator of Stress in Fish," in *Stress and Fish*, ed. Alan D. Pickering (New York: Academic Press, 1981), 11–47.

[46] Riu Oliveira and Leonor Galhardo, "Psychological Stress and Welfare in Fish," *Annual Review of Biomedical Science* 11 (2009): 1–20; Tim Ellis et al., "Cortisol and Finfish Welfare," *Fish Physiology and Biochemistry* 38 (2012): 163–188. Cortisol measurements in a single point of time are of little value for evaluation of stress levels in fish, because studies should take into account circadian and seasonal fluctuations as well as environmental and genetic factors.

harmful conditions, the already mentioned catecholamines cause general reactions of physiological effort – fight or flight – namely, rise blood pressure, accelerate heart rate, and increase blood glucose levels. All mentioned endocrine symptoms accompany aversive emotional states, such as anxiety, fear, or panic. Apart from the physiological stress, researchers demonstrated that, for instance, zebrafish experience emotions of stress and anxiety, and this was proven by a behavioural expression of those negative affects, confirmed by elevated corticosteroids levels, and expressed in such behavioural patterns as a loss of motivation for exploratory behaviours, an increase in scototaxis, that is, searching for a shelter in a dark place, intense thigmotaxis, that is, swimming along tank walls, irregular swimming with sudden immobility (involuntary fear reflex), and disrupted memory processes. As Broom proved, the vertebrate pain system has links between "brain analysers and an output system which can initiate a behavioural or other response. Acute pain could result in behavioural avoidance, repeated risk of acute pain could result in learning so that potential damage could be avoided and chronic pain could result in suppression of activity and behaviour which ameliorates adverse effects."[47]

Furthermore, researchers purposefully caused and conditioned negative emotional states and reactions to prove that fish can also experience mental suffering.[48] Experienced negative emotional states intensified the frequency of nocifensive reflexes, and fear-related behaviours, different escaping responses and avoidance responses may persist for at least seven days past fear-conditioning in zebrafish. This suggests that in the top-down processing, pain sensations and cognitive experiences may be modulated by affective states of the fish, that is, by its mental welfare. If we define emotional reactions as states of body mobilization generated by the action of neuronal modules and circuits, neurochemical substrates, and accompanying physiological changes in the body, then in the light of available study reports we need to agree that fish can at least experience emotions of fear, rage, and contentment.

Final Remarks

There is no doubt that fish are organisms living long enough to apply different learning strategies, and to take advantage of them, for example, when competing

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[47] Donald Broom, "The Evolution of Pain," *Roy. Soc. Med. Int. Cong. Symp. Ser*. 246 (2001): 18.

[48] Caio Maximino et al., "Extending the Analysis of Zebrafish Behavioral Endophenotypes for Modeling Psychiatric Disorders: Fear Conditioning to Conspecific Alarm Pesponse," *Behavioural Processes* 149 (2018): 35–42; Lynne U. Sneddon et al., "Novel Object Test: Examining Nociception and Fear in the Rainbow Trout," *The Journal of Pain* 4, no. 8 (2003): 431–440.

for resources. Moreover the nervous systems of all vertebrates are organized in fundamentally the same way. Even if we infer the experience of pain only from the behaviours of endothermic vertebrates, it is reasonable profoundly to attribute pain experience to reptiles, fish, and amphibians. In all these groups pain seems to be an advantageous experience because it induces reduction in activity level in behaviour which improve the chances that functional reactions can be learnt, associated, and shown so the body damage can be minimized.[49] Therefore, the ability to feel pain has a high adaptive value for fish, and retaining of painful experiences is one of mechanisms of learning. The wide range and diversity of felt sensory percepts – including pain – in consequence of felt and accumulated experiences significantly expands the variety of intelligent reactions in a complex environment. The simplest example confirming this reflection were single administrations of a light electric shock to the carp. The carp remembered which zones they should avoid for several days after just one electric shock.[50] Only after three days, hunger forced them to overcome fear and swim into the zone in which they experienced pain 72 hours earlier.[51] The intensity of pain experiences and feelings of animals represents an indicator of the scale or the severity of mental and physical injuries in a given individual. Then, drastic limitations in meeting instinctive needs of the species or serious body injuries are experienced by fish as acute suffering. Therefore, the intensity and duration of pain in fish are an indicator of the scale of danger in a given situation in which an individual fish currently is, and influence the corresponding short- or long-term retaining of memory traces, to modify its knowledge about the situation, and thus to adapt its behaviour in response to accumulated experiences, sensations, and affects.

A change in the behaviour in response to a foreseen or expected pain or stress stimulus probably occurs through the process of predictive coding of accumulated and retained experiences; however, an analysis of this hypothesis exceeds the scope of this study. However, it should be mentioned that generation of affective components of pain under the influence of predictive processing seems to be confirmed by experiments with stressors conducted in carp, goldfish, salmon, and Cichlids species.[52] The results of those experiments show that the reaction of cortisol secretion also occurs in response to stimuli not causing a direct physical or chemical

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[49] Patrick D. Wall, "On the Relation of Injury to Pain," *Pain* 6, no. 3 (1979): 253–264.

[50] Lynne U. Sneddon, "Pain in Aquatic Animals," *Journal of Experimental Biology* 218, pt 7 (2015): 970.

[51] Rebecca Dunlop et al., "Avoidance Learning in Goldfish (*Carassius auratus*) and Trout (*Oncorhynchus mykiss*) and Implications for Pain Perception," *Applied Animal Behaviour Science* 97, nos. 2–4 (2006): 255–271.

[52] Viktoria R. Mileva et al., "The Stress Response of the Highly Social African Cichlid *Neolamprologus pulcher*," *Physiological and Biochemical Zoology* 82, no. 6 (2009): 720–729.

injury. This, in turn, proves that certain experiences are interpreted and retained for a long time by fish as information about potential and expected dangers. In aversive situations foreseen as highly likely, fish initiate learned anxiety behaviours, including cortisol-based reactions, in accordance with the Mowrer and Miller model. A reduction in cortisol secretion was demonstrated when stressful events occurred in a way foreseeable for fish, when compared to events the exposure to which was unforeseen. This would confirm main assumptions of predictive coding of experiences and affects to reduce uncertainty and eliminate the prediction error.[53] The mechanism for generating the experience of fear is a cognitive adaptation that allows fish to detect threats and respond adequately to the threat. The conscious feeling of fear – at the level of introspective or autonoetic consciousness – is neither required nor necessary for vertebrates and selected invertebrates to respond effectively to expected danger.[54] Most animals oscillate on a *continuum* of sensations, experiences, feelings, and representations at the level of simple anoetic consciousness or perceptual awareness, which is sufficient for simple affective states to perform their function of warning and preventing threats. These affective states, having positive or negative valence and high or low arousal, are also sufficient to place animals experiencing fear and pain in the sentient beings category. In other words, the ability to feel pain, fear and anxiety places the entire species within the framework of ethical reflection as a set of entities that strive to maintain their welfare and that should become beneficiaries of moral concern.[55]

The ethical conclusions appear to be quite clear. The scale of stress, fear, and pain experienced by animals is a measure of our moral care: the more extensive the range of feelings, sensations and experiences in fish, the more evidence we have for the need to include them in the ethical reflection and to ensure for them the greatest wellbeing in conditions of extensive farming. Ichthyologic studies disclosed that the sensory system of *Teleostei* not only can detect harmful stimuli and generate sensory cognitive structures in fish mental landscape, but can also be an indicator for existence of simple, preceptive or (a)noetic conscious states that would characterize that landscape. This level of awareness would be, among others, a result of long-term retaining of sensations, which, in a conceptualized form, enable experiencing emotional reactions, that is, the sensation of pain. A question arises how many more proofs of fish sensitivity and/or fish sentience we need to undertake structured, legal and political activities aimed at combating cruelty to fish. The current

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[53] Giovanni Pezzulo et al., “The Evolution of Brain Architectures for Predictive Coding and Active Inference,” *Philosophical Transactions of the Royal Society B* 377, no. 1844 (2021): 20200531.

[54] LeDoux, *Anxious*, 42–43.

[55] Lynne U. Sneddon et al., “Ample Evidence for Fish Sentience and Pain,” *Animal Sentience* 21, no. 17 (2018): 1–7; Vonne Lund et al., “Expanding the Moral Circle: Farmed Fish as Objects of Moral Cconcern,” *Diseases of Aquatic Organisms* 75, no. 2 (2007): 109–118.

studies concerning pain, fear, and stress in fish clearly emphasize an absolute need to improve methods for farming and effective control of welfare in aquacultures to eliminate too commonly occurring stressors, as confirmed by results of the Compassion In World Farming investigation from the middle of 2023, conducted at four trout farms in Poland.[56]

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[56] See: https://www.ciwf.org.uk/news/2023/10/actor-zoe-wanamaker-unveils-shocking-eu-fish-farm-cruelty.

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