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NEUROTRANSMITTERS AS ECOPOLLUTANTS: IMPACT ON THE FATTY-ACID COMPOSITION AND PHOTOSYNTHETIC PIGMENT CONTENT OF *CHLORELLA VULGARIS*

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Abstract. Neurotransmitters including acetylcholine, serotonin, dopamine, norepinephrine, and histamine represent new-generation ecopollutants and, in addition, endogenous regulatory and signal substances released by the components of natural ecosystems. The goal of the present work was to investigate the effects of neurotransmitters on the fatty-acid composition of membrane lipids and the photosynthetic pigment content of a widely spread phytoplankton component and an indicator organism used for estimating environmental pollution, the green microalga *Chlorella vulgaris*. Strain *C. vulgaris* Beijer was aseptically cultivated under photoautotrophic conditions in modified Tamiya medium. Upon inoculation, all experimental cultures except the control one were supplemented with 1, 10, or 100 µM acetylcholine, serotonin, dopamine, norepinephrine, or histamine. Lipid analysis and fatty acid determination were performed by chromatography with mass spectrometry. Chlorophylls *a* and *b* as well as carotenoids were determined spectrophotometrically. Acetylcholine, dopamine, and norepinephrine increase the total fatty acid content of the lipid of *C. vulgaris* cells whereas histamine and serotonin decrease the fatty acid content. Acetylcholine and histamine statistically significantly augmented the percentage of polyunsaturated fatty acids and decreased that of saturated and/or monounsaturated fatty acids. Serotonin significantly reduced the monounsaturated fatty acids and saturated fatty acids percentage but its influence on the polyunsaturated fatty acids percentage was not statistically verifiable. All tested neurotransmitters increased the photosynthetic content of *C. vulgaris* cells. The data obtained on the effects of neurotransmitters on the biosynthesis of photosystem components and their impact on the fatty-acid composition of *C. vulgaris* lipids resulting in increasing or, conversely, decreasing the monounsaturated fatty acid and saturated fatty acid percentages attest to the prolongation or shortening, respectively, of the early development stages of the microalga's culture. The data are of considerable interest with respect to the interaction of *C. vulgaris* forming a part of the phytoplankton, with various neurotransmitter-producing aquatic organisms including the zooplankton, the fishes, and the higher plants as well as with human-produced neurotransmitter-containing industrial and municipal wastewater.

Keywords: neurotransmitters, biogenic amines, serotonin, dopamine, norepinephrine, histamine, acetylcholine, fatty acids, chlorophyll, carotenoids, *Chlorella vulgaris*, new-generation ecopollutants

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НЕЙРОТРАНСМИТТЕРЫ КАК ЭКОПОЛЛЮТАНТЫ: ВОЗДЕЙСТВИЕ НА СОСТАВ ЖИРНЫХ КИСЛОТ И ФОТОСИНТЕТИЧЕСКИХ ПИГМЕНТОВ *CHLORELLA VULGARIS*

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Аннотация. Нейротрансмиттеры, включая ацетилхолин, серотонин, дофамин, норадреналин и гистамин, являются экополлютантами нового поколения и в то же время как вырабатываемыми компонентами экосистем регуляторными и сигнальными веществами. Целью настоящего исследования было изучение воздействия нейротрансмиттеров на жирнокислотный состав липидов мембран и содержание фотосинтетических пигментов у распространенного компонента фитопланктона и индикаторного объекта экологической обстановки – зеленой микроводоросли *Chlorella vulgaris*. Штамм *C. vulgaris* Beijer асептически культивировали в фотоавтотрофных условиях в модифицированной среде Тамия. При инокуляции во все культуры, кроме контрольных, вносили 1, 10 или 100 мкМ ацетилхолина, серотонина, дофамина, норадреналина или гистамина. Определение жирных кислот проводили методом газовой хроматографии с масс-спектрометрией. Хлорофиллы *a* и *b*, а также каротиноиды определяли спектрофотометрически. Ацетилхолин, дофамин и норадреналин увеличивают общее содержание жирных кислот липидов в клетках *C. vulgaris*, тогда как гистамин и серотонин уменьшают их содержание. Ацетилхолин и гистамин статистически значимо повышали процентное содержание полиненасыщенных жирных кислот за счет снижения такового насыщенных и/или мононенасыщенных жирных кислот. Серотонин значимо снижал долю мононенасыщенных жирных кислот и насыщенных жирных кислот, но влияние на полиненасыщенные жирные кислоты не было достоверным. Все испытанные вещества увеличивали содержание фотосинтетических пигментов клеток *C. vulgaris*. Показанное действие нейротрансмиттеров на биосинтез компонентов фотосистем и на жирнокислотный состав липидов *C. vulgaris* с повышением или, наоборот, снижением доли мононенасыщенных жирных кислот и насыщенных жирных кислот указывает на, соответственно, продление или сокращение ранних стадий развития культур микроводоросли. Полученные данные представляют интерес с точки зрения взаимодействия хлореллы как части фитопланктона с различными выделяющими биогенные амины водными организмами (зоопланктон, рыбы, высшие растения) и с содержащими нейротрансмиттеры индустриальными и муниципальными сточными водами.

Ключевые слова: нейротрансмиттеры, биогенные амины, серотонин, дофамин, норадреналин, гистамин, ацетилхолин, жирные кислоты, хлорофилл, каротиноиды, *Chlorella vulgaris*, экополлютанты нового поколения

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Introduction

The present work is concerned with the effects of neuroactive compounds such as biogenic amines (BAs) on the growth-related and biochemical characteristics of green microalgae. This work is directly related to one of the most rapidly developing subfields of modern ecology, *environmental toxicology* that focuses on the detrimental effects of physical, chemical, and biological factors on living organisms as well as their populations and ecosystems [1]. Among various toxic factors, the environment including water bodies is increasingly affected by active pharmaceutical ingredients (APIs). These substances enter the environment with the wastewater of hospitals and other healthcare institutions, pharmaceutical, cosmetic, and food-producing factories, and municipal sewage systems. Some types of APIs are present in the environment in amounts that exceed the safe levels (maximum acceptable concentrations, MACs). These potentially environment-endangering APIs include neuroactive substances such as antidepressants, antihistamine preparations, β-adrenoreceptor antagonists, anesthetics, calcium channel blockers, etc. [2]. Aquatic ecosystems are affected by very low concentrations of some APIs because they are identical with or homologous to the signal molecules of diverse hydrobionts. "Presumably, a wide spectrum of aquatic organisms including bacteria, algae, invertebrates, and fishes have receptors for such neuroactive pollutants, and this accounts for their responses to these compounds. Specifically, widely used psychopharmacological preparations such as Prozac (an antidepressant) and amphetamines (cognitive capacity stimulants) cause major disruptions in the functioning of bacterial and algal communities within aquatic ecosystems" [3].

Evolutionarily conserved compounds that perform signaling and regulatory functions in various components of aquatic ecosystems include the neurotransmitters (reviewed [3]) that have been tested in the present work for their toxic effects on a model organism, the microalga *Chlorella vulgaris*. These are acetylcholine and the biogenic amines serotonin, histamine, norepinephrine, and dopamine. These compounds are not included in the official lists of globally dangerous APIs and they relatively rapidly decompose in the aquatic environment. However, they are likely to be constantly released into the environment with the wastewater of pharmaceutical factories, healthcare institutions, and food-producing plants.

Dopamine, norepinephrine, and serotonin are known to be produced by pharmaceutical enterprises in Russia and other countries. For instance, dopamine as a cardiotonic and hypertensive preparation is supplied by the Promomed company in Russia and Admed Arzneimittel in Germany. Acetylcholine (Brain Food™) is utilized as a food additive. Food industry wastewater inevitably contains neurotransmitters that are present in the blood and other biological liquids of animals (notably, 0.5 to 1.5 µM serotonin is contained in the human blood, [4]). Histamine accumulates in food items during their storage, due to the bacterial conversion of histidine to histamine. In addition, neurotransmitters are secondarily produced and accumulated in natural ecosystems under the influence of other humankind-produced ecotoxicants including APIs. For instance, the release of cocaine and other neuroactive pollutants into rivers, e.g., the River Thames in London [5], results in increasing the dopamine concentrations in the organism of eels and other fishes that release dopamine into the environment under stress or after an injury.

In this work, humankind-produced neurotransmitters in the environment are considered in connection with their endogenous production by the components of natural ecosystems including unicellular organisms that use them as signals and regulatory agents. It is the "molecular mimicry" of human-produced neuroactive pollutants that resemble endogenous signals and regulators that is a prerequisite for their sufficiently strong ecotoxic effects even at very low concentrations. Such effects were demonstrated in the experimental section of the present work in which a green microalga was used as the test subject.

An important specific type of intercellular communication is referred to as quorum sensing (QS) that subsumes various mechanisms of density-dependent regulation of physiological, biochemical, genetic, and behavioral characteristics of microorganisms in a population. Over the course of the last decades, the main classes of quorum sensing signals were characterized, including aromatic signal molecules (exemplified by AI-3) that operate in enterobacteria and other microorganisms and are structurally similar (homologous) to catecholamines, a group of amines functioning as neurotransmitters and hormones in animals and humans [6].

Therefore, research on the effects of neurotransmitters including, specifically, biogenic amines (BAs) in microalgae is not only of ecotoxicological importance. It also is of much interest in terms of communication between microalgae and other organisms in aquatic or soil ecosystems in which microalgae occur in nature. The dependence of microbial culture growth on the availability of BAs in the medium was predominantly investigated with respect to bacteria, and less attention was paid, in terms of BA effects, to such eukaryotic microorganisms as microalgae as well as to an important subgroup of prokaryotes, cyanobacteria. There is only fragmentary data exemplified by the effects of acetylcholine on the microalgae of the genus *Chlorella* [7, 8] and of dopamine on *Haematococcus lacustris* [9].

The model organism utilized in this work as the test subject, *Chlorella vulgaris,* finds wide application as an indicator organism for estimating the environmental toxicity of various human-produced pollutants.

As for currently available literature data on the impact of neurotransmitters on microalgae, it was demonstrated in the literature that acetylcholine stimulated the growth of *Chlorella* spp. if applied at concentrations between 0.1 µM and 10–100 µM [7, 8], and promoted intracellular accumulation of lipids with double bonds, especially containing a biotechnologically important component, α-linolenic acid [8]. Acetylcholine increased chlorophyll *a* and *b*, monosaccharide and cobalamine (vitamin B_{12}) synthesis in *C. vulgaris* [7]. Choline, the direct precursor of acetylcholine, and its derivatives also promote chlorella growth and lipid accumulation in the biomass, albeit at higher concentrations than acetylcholine [7]. The sulfur-containing neurotransmitter taurine that bears chemical similarity to acetylcholine exerts a stimulatory influence on the growth and chlorophyll and carbohydrate synthesis in *C. vulgaris* [7]. In the green microalga *Haematococcus lacustris*, dopamine enhanced the yield of the biotechnologically valuable carotenoid astaxanthin against the background of NaCl-induced stress (that stimulated astaxanthin synthesis per se); dopamine also promoted biomass accumulation by *H. lacustris* [9].

In the literature, data are also available on endogenous neurotransmitters in microalgae. For instance, *Micrasterias denticulata,* a unicellular green alga of the order Desmidiales, is capable of light-dependent acetylcholine production, based on the data obtained using high-performance liquid chromatoraphy with mass spectrometry [10, 11]. Histochemical studies revealed the presence of endogenous serotonin in the cells of the diatomic microalga *Ulnaria ulna*. Presumably, serotonin is involved in the stress response of this microalga; in all likelihood, serotonin and its acetylated and methylated derivative, melatonin, function as antioxidants [12]. Histamine and acetylcholine were also histochemically detected in *U. ulna* cells [12]. In the cells of the charophyte *Chara australis*, diurnal oscillations in serotonin and melatonin concentrations were documented. The oscillation rhythm of the regulatory agents was different under "long-day" (12 h light: 12 h dark) and "short-day" (9 h light: 15 h dark) conditions [13].

It was established by us earlier that biogenic amines exert a stimulatory effect on the growth-related characteristics of the green microalga *Chlorella vulgaris*. Serotonin (10 μM), dopamine (10 μM), and especially histamine (1 or 10 μM) promoted biomass accumulation by a *C. vulgaris* culture. Micromolar concentrations of biogenic amines also facilitated biomass accumulation by another green microalga, *Scenedesmus quadricauda* [14, 15]. It was also established [16] that norepinephrine and acetylcholine stimulated chlorophyll and carotenoid synthesis in the tested strains of *H. lacustris* (BM-1 and IPPAS H-239); histamine and dopamine promoted these processes only in strain BM-1. As for strain IPPAS H-239, histamine, serotonin, and dopamine decreased their chlorophyll and carotenoid contents concomitantly.

The goal of the present work was to investigate the impact of the neurotransmitters acetylcholine, histamine, serotonin, dopamine, and norepinephrine on the fatty acid composition of the cell lipids of *C. vulgaris* and the pigment (chlorophyll and carotenoid) content in the cells of this microalga.

Materials and methods

The strain *Chlorella vulgaris* Beijer (obtained from the Microbial Culture Collection of the Microbiology Division, Biology Department, Moscow State University) was aseptically cultivated in flasks at 65 μmol PAR photons m^{-2} s^{-1} with constant aeration by filtered atmospheric air at 24 °C in the modified Tamiya medium described in [14, 15]. An exponentially growing culture was used as the inoculum. It was diluted by the medium to a final cell concentration of 1.4×10^6 cells per cm^3, which corresponded to an optical density (OD) of 0.11 ± 0.1 at $\lambda = 750$ nm. The culture was grown until the cell concentration approached a plateau level, which was attained on day 3 of cultivation.

The experimental systems (in which the algae grew in the presence of neurotransmitters) contained 1, 10 or 100 μM of acetylcholine, dopamine, histamine, norepinephrine, or serotonin that were added in the form of hydrochlorides at inoculation as freshly prepared aqueous solutions. It was earlier demonstrated that supplementary post-inoculation addition of neurotransmitters produced no extra effects [17]. The control system (in which the algae grew without neurotransmitters) was supplemented with an equal volume of water at inoculation. All neurotransmitters were analytic grade, purchased from the Sigma company (St. Louis, MO, USA).

The pigments and fatty acids of *C. vulgaris* cultures were analyzed according to the method described in [18]. In stationary-phase cultures (day 3 of cultivation), the cells were pelleted by centrifugation, transferred to a glass–glass homogenizer and disrupted in a chloroform–methanol (10 mL, 2:1, v/v) mixture. The lipid fraction (that also contained pigments) was extracted. Chlorophyll *a* and *b* contents were determined using absorption coefficients for their chloroform solutions [19]. Fatty acid determination was performed using gas chromatography of their methyl esters [20]. The methyl esters were separated and identified according to retention times of pure standards (Sigma, St. Louis, MO, USA) and by characteristic mass spectra obtained with an Agilent 7890 gas chromatograph equipped with a 30-m HP5MS UI capillary column coupled with an Agilent 5970 mass-selective detector (Agilent, Santa Clara, CA, USA).

Four to five independent replicates of each experiment were performed; the mean values are presented in tables and graphs unless stated otherwise. The data obtained for each experimental system were averaged, and the standard deviations were calculated. Most data groups did not conform to the normal distribution pattern and were analyzed using IBM SPSS Statistics R27 0.1.0 software. The Kruskal-Wallis *H* test was applied for three or more independent data groups [21].

Results

Impact of biogenic amines on the fatty acid composition of the cell lipids of *Chlorella vulgaris*. The microalga under study is characterized by high lipid content, including triacylglycerols with predominantly saturated fatty acids that accumulate during the later stages of development of a batch culture [22, 23]. At the earlier stages, microalgal lipids are enriched in unsaturated lipid acids. Research on the effects of environmental pollutants, including those of the new generation, on the ratio between different fatty acid types can shed light on their impact on the rate of the transition between different culture development stages. By influencing the growth dynamics of microalgae that form a part of the phytoplankton as the primary producer, neurotransmitters are expected to affect the rhythm and tempo of the development of aquatic ecosystems.

Acetylcholine. Table 1 contains the total fatty acid content (per 1 g of dry weight) and the percentages of various fatty acid species in *C. vulgaris* cultures grown with and without acetylcholine. From this table, the following conclusions can be drawn:

- Acetylcholine at a concentration of 10 μM statistically significantly increased the fatty acid content of *C. vulgaris* cells, in compliance with the literature data on a different *Chlorella* species, *C. sorokiniana* [16] as well as with our earlier work on the microalga *S. quadricauda* [38]; in contrast, acetylcholine at a higher concentration (100 μM) brought about a decrease in fatty-acid content.

- Acetylcholine increased the percentage of polyunsaturated fatty acids (PUFAs).
- Acetylcholine decreased the percentages of saturated and monounsaturated fatty acids (SFAs and MUFAs, respectively).

Histamine. It is evident from Table 2 that:

- Histamine significantly decreased the total fatty acid content in the cells.
- Histamine increased the percentage of PUFAs and decreased that of SFAs (at a concentration of 10 μM); as for individual fatty acid species (not shown in the Table 2), the percentages of stearic and myristic acid were reduced by 45 % and 18 %, respectively, with 1 μM histamine of some unsaturated fatty acids.
- Histamine only caused a statistically insignificant decrease in MUFA percentage.

Table 1

Fatty acid content of *C. vulgaris* cultures grown with or without acetylcholine (ACh). Kruskal-Wallis test results with independent samples for the experimental and control groups indicate significant differences between the data groups to be compared

Fatty acid	Proportion in total fatty acids, %			
	Control	ACh, 1 μM	ACh, 10 μM	ACh,100 μM
Saturated fatty acids (SFAs)	28.2 ± 0.9	26.6 ± 0.8	26.6 ± 0.9	23.9 ± 0.8
Monounsaturated fatty acids (MUFAs)	15.3 ± 0.8	13.4 ± 0.7	13.9 ± 0.7	11.4 ± 0.7
Polyunsaturated fatty acids (PUFAs)	56.5 ± 1.0	60.0 ± 1.1	59.5 ± 1.1	64.7 ± 1.2
Total fatty acid content, mg/g of dry weight	*62.4 ± 2.0*	*60.6 ± 1.9*	*69.5 ± 1.9*	*54.7 ± 1.9*

Table 2

Fatty acid content of *C. vulgaris* cultures grown with or without histamine (His). Kruskal-Wallis test results or the experimental and control groups demonstrate that only the differences between the experimental and control groups for MUFAs are not significant

Fatty acid	Proportion in total fatty acids, %			
	Control	His, 1 μM	His,10 μM	His, 100 μM
Saturated fatty acids (SFAs)	31.6 ± 0.9	33.1 ± 1.0	38.6 ± 1.0	30.9 ± 0.9
Monounsaturated fatty acids (MUFAs)	23.7 ± 0.7	11.7 ± 0.6	11.6 ± 0.7	11.9 ± 0.7
Polyunsaturated fatty acids (PUFAs)	43.9 ± 1.1	54.4 ± 1.2	48.9 ± 1.1	56.3 ± 1.2
Total fatty acid content, mg/g of dry weight	*79.3 ± 1.0*	*44.2 ± 1.0*	*43.7 ± 0.9*	*49.7 ± 1.1*

Serotonin. This neurotransmitter:

- Decreased the total fatty acid content in *C. vulgaris* lipids, although to a lesser extent than histamine (Table 3).
- Based on the results of the Kruskal-Wallis test, it only insignificantly increased the PUFA percentage, even though serotonin brought down to zero the contribution of γ-linolenic acid; with 100 μM serotonin, the lipids also lacked 20:2, 20:3, and 20:4 fatty acids (data on individual fatty acids are not contained in the Table 3).
- Serotonin verifiably lowered the MUFA and, to a lesser extent, SFA percentage (although this does not concern the percentage of arachic acid, not shown).

Table 3

Fatty acid content of *C. vulgaris* cultures grown with or without serotonin (5-HT). Kruskal-Wallis test results indicate that only the differences between the experimental and control groups for PUFAs are not significant

Fatty acid	Proportion in total fatty acids, %			
	Control	5HT, 1 μM	5HT,10 μM	5HT, 100 μM
Saturated fatty acids (SFAs)	31.0 ± 1.0	27.8 ± 0.9	28.1 ± 1.0	27.1 ± 0.9
Monounsaturated fatty acids (MUFAs)	9.06 ± 0.5	5.88 ± 0.6	6.19 ± 0.55	6.9 ± 0.6
Polyunsaturated fatty acids (PUFAs)	59.9 ± 1.4	66.3 ± 1.5	65.7 ± 1.7	66.0 ± 1.4
Total fatty acid content, mg/g of dry weight	*84.4 ± 1.0*	*72.1 ± 0.9*	*73.2 ± 1.0*	*68.9 ± 0.9*

Dopamine. The data shown in Table 4 are as follows:

- Dopamine at a concentration of 10 μM significantly increased the total fatty-acid content in *C. vulgaris* cells.
- The dopamine-caused slight decrease in PUFA content proved insignificant statistically.
- Dopamine produced no verifiable effect on the MUFA and SFA percentages.

Norepinephrine. Like dopamine, norepinephrine belongs to catecholamines, and only the presence of one hydroxy group in the side chain distinguishes norepinephrine from dopamine. The data obtained are as follows (Table 5):

- Norepinephrine at a concentration of 1 µM slightly increased, and at higher concentrations decreased the total fatty-acid content, these effects being statistically significant.
- Norepinephrine only insignificantly increased the PUFA percentage and decreased the MUFA and SFA percentages.

Table 4

Fatty acid content of *C. vulgaris* cultures grown with or without dopamine (DA).
Kruskal-Wallis test results indicate that only the differences between
the experimental and control groups for total fatty acid content are significant

Fatty acid	Proportion in total fatty acids, %			
	Control	DA, 1 µM	DA,10 µM	DA, 100 µM
Saturated fatty acids (SFAs)	28.2 ± 1.0	28.0 ± 0.9	28.7 ± 0.9	29.7 ± 1.0
Monounsaturated fatty acids (MUFAs)	5.7 ± 0.5	6.1 ± 0.6	7.1 ± 0.6	6.2 ± 0.5
Polyunsaturated fatty acids (PUFAs)	66.0 ± 1.4	65.9 ± 1.6	64.1 ± 1.4	64.1 ± 1.5
Total fatty acid content, mg/g of dry weight	*60.7 ± 1.1*	*59.7 ± 1.0*	*68.5 ± 1.2*	*61.7 ± 1.0*

Table 5

Fatty acid content of *C. vulgaris* cultures grown with or without norepinephrine (NE).
Kruskal-Wallis test results indicate that only the differences between
the experimental and control groups for MUFAs are significant

Fatty acid	Proportion in total fatty acids, %			
	Control	NE, 1 µM	NE,10 µM	NE, 100 µM
Saturated fatty acids (SFAs)	35.7 ± 1.0	31.0 ± 0.9	37.1 ± 1.0	36.2 ± 1.1
Monounsaturated fatty acids (MUFAs)	7.9 ± 0.5	5.8 ± 0.4	8.3 ± 0.5	7.9 ± 0.4
Polyunsaturated fatty acids (PUFAs)	56.4 ± 1.3	63.3 ± 1.4	54.6 ± 1.3	55.8 ± 1.2
Total fatty acid content, mg/g of dry weight	*60.7 ± 1.0*	*68.8 ± 1.3*	*54.3 ± 1.0*	*53.1 ± 0.9*

According to the data presented in this subsection, acetylcholine (at a concentration of 10 µM only), dopamine, and norepinephrine (at a concentration of 1 µM only) increased the total fatty acid content in *C. vulgaris* cells. Serotonin and histamine decreased this content. Acetylcholine and histamine statistically verifiably augmented the PUFA percentage at the expense of the SFA and/or MUFA percentage. Serotonin significantly reduced the MUFA and SFA share, although the PUFA increase proved insignificant, based on Kruskal-Wallis test results. Dopamine and norepinephrine failed to exert a statistically verifiable effect on the ratio between fatty acid types.

Impact of biogenic amines on the photosynthetic pigments of *C. vulgaris* Microbial oxygenic phototrophs (microalgae) are believed to be very efficient solar energy converters. This is one of the reasons why investigating parameters related to photosynthetic efficiency is biotechnologically relevant. The following is the data of this work on photosynthetic pigments in the tested microalgae with and without neurotransmitters.

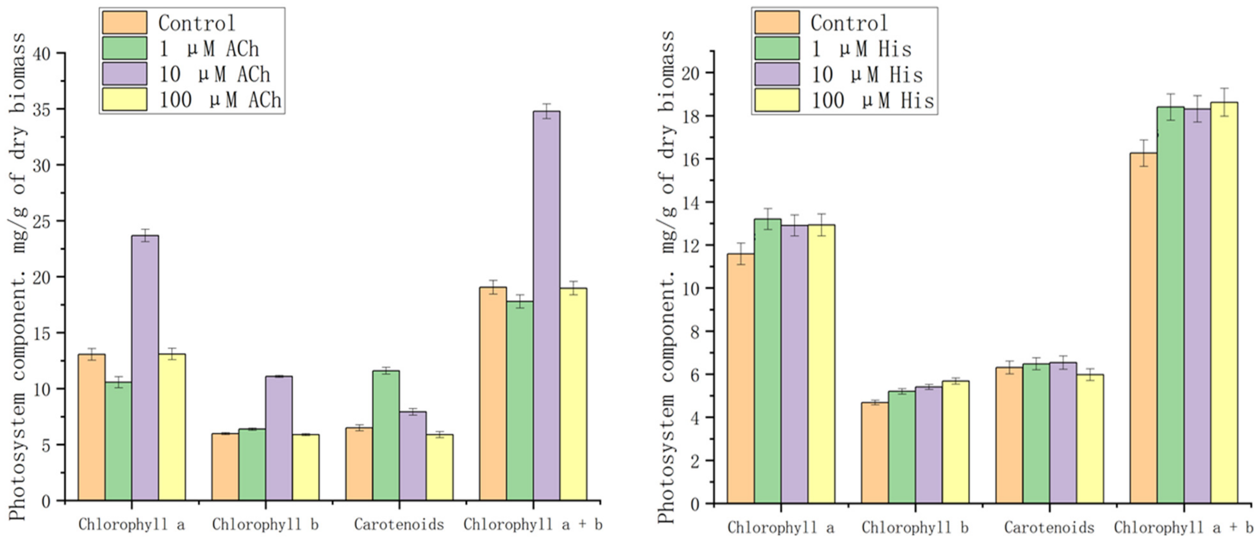
Acetylcholine (Fig. 1,*A*). When applied at the lowest concentration (1 µM), acetylcholine somewhat decreased the chlorophyll a content, thereby also reducing the total chlorophyll *a*+*b* amount; it also increased the carotenoid content. At a concentration of 10 µM, acetylcholine markedly increased both the chlorophyll *a* and *b* content, whereas the carotenoid content was virtually the same as in the control samples. At the highest tested concentration (100 µM), the total chlorophyll content returned to its control level, and the carotenoid content was somewhat decreased.

Histamine insignificantly increased the total chlorophyll content in *C. vulgaris* cells without considerably influencing their carotenoid content (Fig. 1,*B*).

Serotonin as well as *norepinephrine* increased the chlorophyll *a*+*b* content and, to a lesser extent, the carotenoid content (at concentrations of 10 and 100 µM) (Fig. 2,*A*,*B*, respectively).

Dopamine produced a minor but statistically verifiable effect on the chlorophyll content without affecting the carotenoid content (Fig. 3).

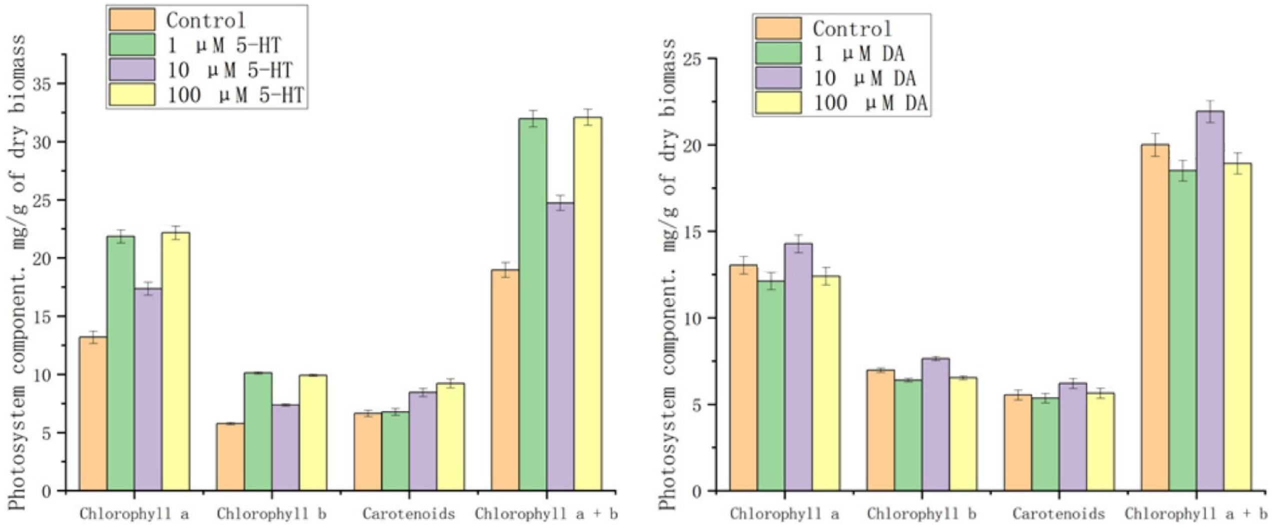
In summary, all tested substances increased, to some extent, the photopigment content and, therefore, probably the photosynthetic activity of *C. vulgaris* cells, which is consistent with the earlier work revealing the stimulatory effects of the neurotransmitters on the growth of this alga [14]. The data obtained are also in line with the literature data on the acetylcholine effect on microalgae [7, 8].



A)

B)

Fig. 1. Impact of acetylcholine (Ach, *A*) and histamine (His, *B*) on the pigment content in *C. vulgaris* cells. Kruskal-Wallis test results indicate that all differences between control and experimental data are significant



A)

B)

Fig. 2. Impact of serotonin (5-HT, *A*) and dopamine (DA, *B*) on the pigment content in *C. vulgaris* cells. Kruskal-Wallis test results indicate that all differences between control and experimental data are significant, except the carotenoid data (*B*)

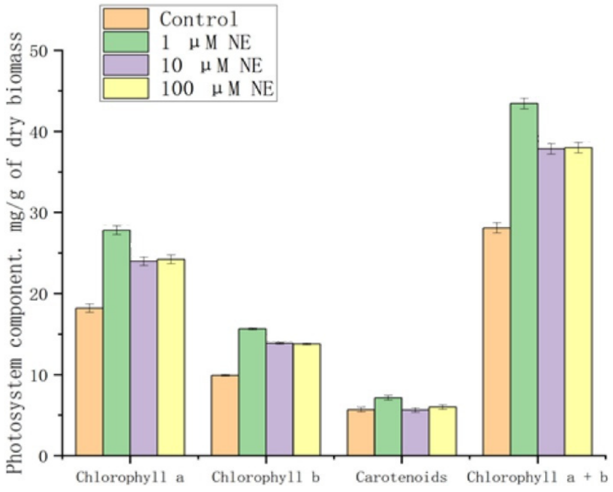


Fig. 3. Impact of norepinephrine (NE) on the pigment content in *C. vulgaris* cells. Kruskal-Wallis test results indicate that all differences between control and experimental data are significant

Discussion

The present work is concerned with the effects of neuroactive biogenic amines, potentially important new-generation environmental toxicants, on the fatty-acid composition of the lipids and the photosynthetic pigment content in the eukaryotic green microalga *Chlorella vulgaris*. It was revealed that the tested neurotransmitters dopamine, norepinephrine, serotonin, histamine, and acetylcholine significantly influenced (either increased or decreased) the fatty-acid content in the cells of this typical phytoplankton representative and indicator organism widely used to estimate the human-produced pollution level. Acetylcholine proved to promote fatty acid synthesis in *C. vulgaris,* similar to other microalgae tested earlier [16, 24]; the statistically verifiable effects of other neurotransmitters vary depending on the microalgal species involved.

Even though the data available in the literature on the role of neurotransmitters in microalgae are insufficient (the data were summarized in the Introduction), there is a large body of evidence regarding the effects of phytohormones that are chemically and functionally similar to neurotransmitters. At low concentrations, varuious subgroups of phytohormones (auxins, gibberellins, cytokinins, brassinosteroids, ethylene, abscisic, salicylic, and jasmonic acid, etc.) exert a stimulatory influence on the growth of microalgae, biosynthesis of valuable products by them, and their stress resistance [26–30]. In the literature, the following mechanisms of stimulatory action of phytohormones on microalgal growth are posited:

1. Antioxidant effect that is linked to the activation of enzymes that quench reactive oxygen species and to an increase in the concentrations of antioxidants such as ascorbic acid and glutathione [28]. Some neurotransmitters, especially serotonin, are chemically related to such plant hormones as auxins. Serotonin oxidation results in the formation of a substituted auxin, 5-hydroindole-3-acetic acid.

2. Promotion of photosynthetic activity by increasing the photosynthetic pigment content, which, in turn, implies an increase in gene expression that is related to chlorophyll and carotenoid synthesis [28].

3. Influence on the dynamics and rhythms of development of microalgal cultures. Phytohormones are known to exert a regulatory influence on biorhythms and the dynamics of undergoing "age-related" stages in the development of plants. For instance, abscisic acid and ethylene promote leaf shedding, suppress growth processes, and accelerate plant senescence [29, 30].

Presumably, all the three mechanisms contribute to the effects of neurotransmitters. Significant importance should be attached to neurotransmitters' antioxidant activity that is characteristic, for instance, of serotonin that may prevent the peroxidation of the unsaturated fatty acids of membrane lipids, in an analogy to the stimulating effects of phytohormones including the aforementioned auxins on enzymatic and non-enzymatic reactive oxygen species (ROS)-quenching systems in microalgae [27].

Option (2) in the above list is directly supported by our data that all tested neurotransmitters statistically verifiably increased the chlorophyll concentrations in *C. vulgaris* cells. The neurotransmitters also raised the concentrations of carotenoids as light-harvesting antenna components, except for dopamine that exerted a statistically insignificant influence.

The fatty acid data of the present work lend support to option (3) in the above list on this page. Acetylcholine and histamine verifiably increased the PUFA share (Tables 1, 2). Serotonin reduced the MUFA and SFA percentage even though its influence on the PUFAs could not be verified using the Kruskal-Wallis test (Table 3). In combination with the data on an increase in photosynthetic pigment contents, the results are interpretable in terms of the suggestion that these neurotransmitters influence the developmental dynamics of the *C. vulgaris* culture. They prolong the earlier stages that are characterized by more active photosynthesis and more unsaturated lipids in the membranes

In similar fashion, studies with another green microalga, *Scenedesmus quadricauda*, revealed [24] that acetylcholine, histamine, and norepinephrine enhanced the PUFA content and plausibly prolonged its earlier developmental stages.

As far as the mechanism of action of the tested neurotransmitters is concerned, it seems likely that they bind to respective membrane receptors in microalgal cells. Presumably, microalgae possess analogs of quorum sensing (QS) systems that are widely spread in the microbial realm (see review [6]). The neurotransmitters that were tested in this work operate in microbial QS systems, enabling microorganisms to estimate the density of their population from the concentrations of QS signals (autoinducers, or pheromones) released by microbial cells. For instance, catecholamines (dopamine and norepinephrine) are functionally analogous to QS signal AI-3. Similar to this signal, catecholamines are recognized by receptor histidine kinases QseC and QseE in *Escherichia coli*. Signal binding to receptors promotes the expression of gene groups (operons) that are necessary for growth processes and for the synthesis of products involved in the interaction between microorganisms and the host organism or other ecosystem components (reviewed, [31]).

The data on the impact of neurotransmitters on fatty acid and pigment contents in *C. vulgaris* at low (micromolar) concentrations give grounds for the suggestion that this eukaryotic microalga possesses an analog of bacterial QS systems, and this microalgal quasi-QS system binds neurotransmitters as specific signals. Interaction between some of the tested neurotransmitters and the receptors may result in promoting fatty acid desaturase activity. This should phenomenologically manifest itself in prolonging earlier developmental stages with a high fatty acid desaturation degree.

Of note is the fact that high neurotransmitter concentrations may produce effects that are qualitatively different from those of lower neurotransmitter concentrations. For instance, acetylcholine (Table 1) and dopamine (Table 4) increase the total fatty acid content at a concentration of 10 μM (and norepinephrine at a concentration of 1 μM, Table 5) but not at a concentration of 100 μM. Apparently, neurotransmitters applied at relatively high concentrations can function as uncouplers collapsing the membrane potential, since they can cross membranes in the form of ions. This effect was demonstrated in experiments on the effects of serotonin on the membranes of the purple phototrophic bacterium *Rhodospirillum rubrum* [17].

Therefore, neurotransmitters can be considered new generation environmental pollutants (toxicants) that are recognized by natural ecosystem components as analogs of endogenous regulatory and signals and, therefore, affect whole natural ecosystems at very low concentrations (as "trace amounts"). Both the inhibitory and stimulatory effects of neurotransmitters on microalgae can result in doing serious harm to ecosystems. Inhibition of fatty acid biosynthesis in microalgae by some of the tested neurotransmitters (histamine and serotonin) poses the threat of disrupting phytoplankton-dependent trophic chains in ecosystems. Stimulation of the biosynthesis of photosystem components by neurotransmitters (see Fig. 1–3) is fraught with causing uncontrollable algal blooming and the eutrophication of natural or artificial (aquacultural) water bodies.

The impact of neurotransmitters on the fatty-acid composition and photosynthetic pigment content in microalgal cells can be considered not only in terms of human-produced neurotransmitter effects as environmental pollutants; this impact can also be interpreted with respect to the ongoing chemical interaction between the chlorella that forms a part of the phytoplankton – and various neurotransmitter-releasing aquatic ecosystem components exemplified by the zooplankton, fishes, and aquatic higher plants. There is much evidence that neurotransmitters concomitantly interact with a large number of different ecosystem components, which gives grounds for the suggestion that neurotransmitters form a part of ecosystem-orchestrating regulatory substances, or ecomones [3].

Conclusion

The present work is concerned with the effects of biogenic amines (dopamine, norepinephrine, serotonin, histamine, and acetylcholine) on the fatty acid composition and photosynthetic pigment contents of *Chlorella vulgaris*. It was revealed that acetylcholine, dopamine, and norepinephrine increased the total fatty acid content of *C. vulgaris* lipids, whereas serotonin and histamine decreased it. Acetylcholine and histamine elevated the percentage of PUFAs at the expense of lowering those of SFAs and/or MUFAs; serotonin significantly decreased the MUFA and SFA percentage without producing a verifiable effect on the PUFA content. All tested substances augmented the photosynthetic pigment content of *C. vulgaris*.

The results of this work are hypothetically interpretable in terms of the idea that microalgae possess analogs of quorum sensing systems that are typical of prokaryotes. Interaction between some neurotransmitters and respective receptors may result in promoting fatty acid desaturase activity and, therefore, prolonging the culture development stages that are characterized by a high fatty acid desaturation degree.

In light of the data obtained in this work in conjunction with earlier findings regarding the stimulation of the growth of *C. vulgaris* and other microalgae by neurotransmitters [14–16, 24], it is expectable that microalgal growth will become uncontrollable even under the influence of "trace amounts" of neurotransmitters and their derivatives. Such low concentrations may be present in the parts of water bodies that are relatively remote from the areas in which the wastewater of food or pharmaceutical industrial facilities is released, even though there are natural mechanisms of their inactivation involving biotic (enzymatic degradation) or abiotic (photooxidation) processes. Based on the data obtained, it is strongly suggested to more thoroughly purify potentially "neuroactive" wastewater, in order to prevent water "blooming" and eutrophication.

From the ecological and hydrobiological viewpoint, the effects of neurotransmitters on the biochemical characteristics of *C. vulgaris*, a widespread inhabitant of freshwater bodies, is of considerable interest in conjunction with the data on the growth-promoting effects of neurotransmitters that were obtained earlier [14, 15, 24] in terms of the involvement of neurotransmitters in multilateral interaction among the components of the ecosystems of natural or artificial water bodies.

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