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EXAMINATIONS ON THE FAT METABOLISM IN FRESHWATER FISHES. THE SYMPHATHETIC NERVOUS SYSTEM AND THE MOBILIZATION OF FATTY ACIDS

TIBOR FARKAS

Biological Research Institute of the Hungarian Academy of Sciences, Tihany, Hungary

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Evidence has been presented that the sympathetic nervous system regulates the mobilization of fats from adipose tissue of man and mammals. The denervation of the brown or white adipose tissue decreases the mobilization of fats from the adipose tissue even in starving animals (HAUSBERGER 1934, BEZNÁK 1937). In vivo and in vitro administration of norepinephrine increases the production of free fatty acid in adipose tissue (WHITE et al. 1958). The factors stimulating the activity of the nervous system as: anxiety, the talking about exciting events (BOGDONOFF et al. 1959), cold stress (GIGLEN et al. 1962) or electric shock (CORREL 1963) increase the free fatty acid level in the blood plasma. Adrenerg blocking agents block the adipokinetic effect of catecholamines in rat, man and in dog (HAVEL et al. 1959, ZSOTER et al. 1966, SHOTZ et al. 1960, BOGDONOFF et al. 1959). The increase of plasma free fatty acids after physiologic arousal (BOGDONOFF et al. 1960) or the effect of electric stimulation, can be antagonized by sympathectomy (CORREL 1963).

The teleost fishes have a morphologically well-developed sympathetic nervous system (NICOL 1951). The presence of catecholamines in the nerves and different organs of several fish species had already been demonstrated (EULER 1961 et al. ÖSTLUND 1954, CHAVIN 1966). The effect of epinephrine and norepinephrine on the activity of heart (FÄNGE et al. 1954), on gill vessels (FÄNGE 1962) and on blood pressure (MOTT 1957) has already been reported. Catecholamines have the same effect on iris or on intestinal smooth muscle as in the mammals (YOUNG 1933, EULER et al. 1957). No data are yet available on how the metabolic processes are regulated through these compounds.

In our previous work it had already been shown that intensive lipolysis takes place in the adipose tissue of the carp *Cyprinus carpio* L., but the tested lipolytic hormones (epinephrine, norepinephrine, isopropylnorepinephrine, adrenocorticotroph hormone) were ineffective in raising plasma free fatty acid levels (FARKAS 1967). The investigations were extended to other fish species, too. In the present paper we report more data on the effect of norepinephrine on the fat metabolism in fishes. It is hoped that the results might be of value not only for better understanding of the fat metabolism of fishes but also for the understanding of lipid mobilization in general.

Materials and method

The experiments were carried out on the following fish species: carp *(Cyprinus carpio* L.), bream *(Abramis brama* L.*)*, perch *(Perca perca* L.), pike-perch *(Lucioperca lucioperca* L.), shad *(Pelecus cultratus* L.). The weight of the carps was 4—500 g, that of the bream and of the pike-perch 250—300 g; the others weighed 80—100 g. Except the carps, the other fish species were collected in the Lake Balaton 2—6 days before the experiment. The carps were purchased from a near-by fish-hatchery. After collecting they were kept in 200 l aquaria, 5 in each fish-tank. No food was given to the animals in captivity.

For the in vivo experiments norepinephrine bitartarate (2 mg/fish) dissolved in olive-oil or carboxy-methylcellulose was injected intramuscularly 2 hours before the death of the animals. The control animals received solvent only.

The in vitro experiments were carried out on the adipose tissue surrounding the intestine or the swim bladder. After killing the animals, the adipose tissues were quickly removed and placed into a physiological solution. The tissues were then cut into pieces of 50—60 mg; 200 mg of them were incubated for one hour in Krebs-Ringer phosphate buffer solution at pH 7.4, in the presence or absence of norepinephrine. The physiological solution contained only 0.48% NaCl. Other tissue pieces were homogenized in n-heptane at the beginning of the incubation in order to determine the free fatty acid content of the adipose tissue. At the end of the incubation the incubated adipose tissues were also homogenized in n-heptane. No fatty acid acceptor was added to the incubation medium. Under such circumstances, as in the case of the mammals, the produced fatty acids accumulate in the adipose tissue. 2—3 incubations were carried out simultaneously. The norepinephrine content of the incubation medium was 2 μg/ml.

Cold stress was performed by adding ice to the water of the aquarium sufficient to decrease the temperature of the water from 17 °C to 5 °C within 20 minutes. This temperature was maintained through 2 hours.

In other experiments CO_2 was bubbled into the water of the aquarium, and the fishes were allowed to "sniff" on the surface of the water.

Blood was taken by cutting off the caudal vein and collected in pre-chilled heparinized centrifuge tubes.

The quantity of plasma free fatty acids was determined by DOLE's method (1956) from 0.5—1.0 ml blood plasma. In order to determine the free fatty acid content of the adipose tissue, the homogenizates were diluted to 5.0 ml and from this 1.0 ml aliquot was titrated with 0.01 N NaOH in the presence of brom-thymol-blue indicator.

The glycerol content of the blood plasma was determined colorimetrically by LAMBERT and NEISH (1950) method from 0.1 ml blood plasma that had previously been freed from proteins with 3% $HClO_4$. The blood glucose level, was measured colorimetrically (HYVÄRINEN 1962).

Results

In previous experiments it was shown that norepinephrine and some other lipolytic hormones were ineffective in stimulating the free fatty acid production of the adipose tissue of the carp (FARKAS 1967). As shown in *Table I*, norepinephrine does not stimulate lipolysis in any of the examined fish

species. The free fatty acid content of blood plasma and adipose tissue in the freshly collected bream did not change after administration of the hormone, when, however, the animals had been starved for 3—6 days before the experiment, the free acid content of both the blood plasma and of the adipose tissue has considerably decreased. In these cases the hormone caused strong hyperglycaemia, too. A relationship seems to exist between the glycogenolytic effect of the hormone and the effect on the adipose tissue and plasma free fatty acid levels. However, the situation is not similar to that described by HAVEL et al. (1959) and SHAFIR et al. (1960) on dogs and rats after administration of epinephrine. Epinephrine has caused only initial increase in the plasma free acids in these animals. Parrallel with the increase of blood glucose content the plasma free fatty acid level began to decrease, and when the blood glucose level reached its maximum, the amount of plasma free acids fell back to the control value. In the case of fish (carp-unpublished investigation) no such initial increase could be observed. The glycerol content of the blood did not changed significantly as a result of hormone treatment (carp, control: 0.238 ± 0.05 μM/ml, treated: 0.175 ± 0.04 μM/ml; bream control: 0.346 ± 0.06 μM/ml, treated: 0.231 ± 0.06 μM/ml.

Table 2 presents the results of the in vitro experiments. It appears from these data that the adipose tissues of the examined fish species produced a considerable amount of free fatty acids. In the course of the experiment the quantity of fatty acids was doubled in the adipose tissues. Norepinephrine (2 μg/ml) did not stimulate the free fatty acid production of the adipose tissues The hormone was without stimulating effect if its quantity was raised to 20 μg/ml *(Fig. 1)*. The lipolytic activity of the adipose tissue in the animals

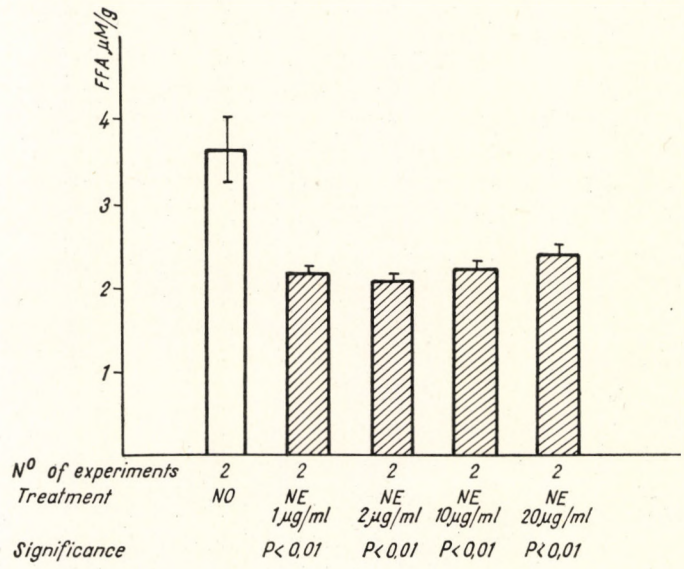

Fig. 1 — 1. ábra

The effect of various doses of norepinephrine on the production of free acios in the adipese tissue of the carpi *Cyprinus carpio L*

Különböző koncentrációju noradrenalin hatása ponty *Cyrinus carpioc L.* zsirszövet szabad zsirsáv termelésése

Table 1 — 1. Táblázat

The in vivo effect of noradrenaline on fatty acid mobilization and on the level of blood glucose in some fresh water fish species

In vivo noradrenalin hatása zsírsavmozgósításra és vércukorszintre néhány édesvízi halban

Name	Number of animals	Treatment	Plasma free fatty acid μM/ml	Adipose tissue μM/gl	Blood glucose mg/ml	Notes
Név	Állatok száma	Kezelés	Plazma szabad zsírsav μM/ml	Zsírszövet FFA μM/gl	Vércukor mg/ml	Megjegyzés
Cyprinus carpio L.	4	Control	1.293 ± 0.035	3.029 ± 0.436	0.330 ± 0.031	Winter — Tél
Cyprinus carpio L.	4	Norepinephrine	1.062 ± 0.094	1.686 ± 0.097	0.706 ± 0.052	
Cyprinus carpio L.	4	Control	0.584 ± 0.018	1.598 ± 0.150	0.548 ± 0.042	Summer — Nyár
Cyprinus carpio L.	4	Norepinephrine	0.403 ± 0.012	1.065 ± 0.217	2.177 ± 0.038	
Abramis brama L.	12	Control	1.138 ± 0.058	6.510 ± 0.181	1.807 ± 0.183	Summer, after collecting — Nyár, fogás után
Abramis brama L.	12	Norepinephrine	0.956 ± 0.015*	6.720 ± 0.477*	2.283 ± 0.171*	
Abramis brama L.	12	Control	0.607 ± 0.041		0.660 ± 0.051	After starvation of 6 days
Abramis brama L.	12	Norepinephrine	0.303 ± 0.025		1.060 ± 0.085	6 nap éhezés után
Lucioperca lucioperca L.	4	Control	1.141 ± 0.242	3.272 ± 0.229	0.430 ± 0.044	Summer — Nyár
Lucioperca lucioperca L.	4	Norepinephrine	0.844 ± 0.041	2.522 ± 0.492	3.308 ± 0.149	

* $P > 0.05 < 0.02$

Table 2. — 2. Táblázat

The in vitro effect of noradrenaline on the free fatty acid production in the fish adipose tissue

Noradrenalin hatása halzsírszövet in vitro szabadzsírsav termelésére

Name	Number of animals	Control t_0 μM/g/h	Control t_{60} μM/g/h	Noradrenaline 2 μg/ml, t_{60} μM/g/h	Notes
Név	Állatok száma	Kontroll t_0 μM/g/h	Kontroll t_{60} μM/g/h	Noradrenalin 2 μg/ml t_{60} μM/g/h	Megjegyzés
Cyprinus carpio L.	4	1.956 ± 0.230	4.350 ± 0.449	3.100 ± 0.244*	Winter — Tél
Cyprinus carpio L.	4	3.933 ± 0.197	7.998 ± 0.672	9.001 ± 0.707	Summer — Nyár
Abramis brama L.	8	6.241 ± 0.259	13.389 ± 0.744	13.100 ± 0.326	Summer — Nyár
Perca perca L.	2	2.385 ± 0.197	5.581 ± 0.479	4.861 ± 0.146	Winter — Tél
Lucioperca lucioperca L.	4	3.295 ± 0.211	6.834 ± 0.479	5.484 ± 0.313*	Spring — Tavasz
Lucioperca lucioperca L.	4	4.001 ± 0.541	8.886 ± 0.415	9.436 ± 0.507	Summer — Nyár
Pelecus cultratus L.	4	2.815 ± 0.163	3.617 ± 0.286	2.807 ± 0.214*	Winter — Tél

* = $P < 0.05$
t_0 = free fatty acid content of the adipose tissue at the beginning of the experiment
t_{60} = free fatty acid content of the adipose tissue at the end of the experiment
t_0 = a zsírszövet szabad zsírsavtartalma a kísérlet elején
t_{60} = a zsírszövet szabad zsírsavtartalma a kísérlet végén

Table 3. — 3. Táblázat

Plasma free fatty acid and blood glucose level in stress conditions

Plazma szabad zsírsav- és vércukorszint stress állapotokban

Name	Number of animals	Types of stress	Plasma FFA μM/ml	Adipose tissue FFA μM/g	Blood glucose mg/ml	Notes
Név	Állatok száma	Stress típusa	Szabad zsírsav μM/ml	Zsírszövet, μM/g	Vércukor, mg/ml	Megjegyzés
Abramis brama L.	5	Control	0,505 ± 0,043		0,597 ± 0,060	$P < 0.01$
Abramis brama L.		Cold — Hideg	0.576 ± 0.049		0.910 ± 0.030	
Lucioperca lucioperca L.	5	Control	1.141 ± 0.081	3.295 ± 0.146	0.430 ± 0.024	$P < 0.01$
Lucioperca lucioperca L.		Cold — Hideg	1.046 ± 0.029	2.965 ± 0.127	1.866 ± 0.076	
Abramis brama L.	8	Control	0.825 ± 0.073		0.587 ± 0.054	$P < 0.01$
Abramis brama L.		injection (phys. sol.) — injekció (fiz. oldat)	0.568 ± 0.005		0.881 ± 0.098	
Cyprinus carpio L.	4	Control	0.640 ± 0.046		0.423 ± 0.033	
Cyprinus carpio L.		injection (phys. sol.) — injekció (fiz. oldat)	0.600 ± 0.090		0.626 ± 0.088	$P < 0.05$
Abramis brama L.	5	Control	0.698 ± 0.052		0.562 ± 0.035	
Abramis brama L.		Anoxia	0.306 ± 0.010		1.307 ± 0.117	$P < 0.01$

caught in summer remained unchanged in the presence of the hormone while the adipose tissues of the animals collected in winter produced less free fatty acids. This is especially evident in the case of the carp and of the pike-perch where both winter and summer experiments are available. The mechanism through which the hormone decreases the free fatty acid production of the tissue, is not yet clear, it is probable that under in vivo and in vitro conditions it is the same.

Table 3 demonstrates that stress conditions like a simple intramuscular injection of physiological solution, exposure to cold or hypoxia do not increase the free fatty acid content of the blood in the examined fish species. On the above-mentioned effects the level of blood glucose was increased like in animals treated with epinephrine. Similarly to mammals, the increase of the blood glucose level might be attributed to elevated sympathetic tonus but the increased secretion of catecholamines in fish, does not lead to the increase of the plasma free fatty acid level. In some experiments, like in the case of norepinephrine the free fatty acid content of the blood plasma has decreased.

Discussion

The following evidences suggest that in the fresh water fishes — similarly to mammals — neutral fats are mobilized in the form of free fatty acids:

1. An intensive lipolysis takes place in adipose tissue incubated in vitro. The produced fatty acids are released to the incubation medium when it contains fatty acid acceptors (FARKAS 1967).

2. Their blood contains an appreciable amount of free fatty acids. The free fatty acid level of the blood plasma seems to depend on the nutritional state of the animal. Prolonged fasting results in an increase of plasma free fatty acid level. Per os administration of glucose to starving animals decreases the level of the plasma free fatty acids.

The production of the free fatty acids in the adipose tissue of mammals is under a complicated metabolic, endocrine and nervous control. The metabolic regulation is realized by shifting the balance of hydrolytic and re-esterification processes in adipose-cells. If the level of blood glucose is high, the intensity of the re-esterification processes increases and the amount of free fatty acids released from the adipose tissue decreases, and vice versa. That in the adipose tissue of the fish, too, a similar mechanism is existing, which is suggested by the observation that glucose in vivo or in vitro decreases the production of free fatty acids. The fact that neither norepinephrine nor emergency conditions increase the production of adipose tissue free fatty acids suggest that the sympathetic nervous system does not play a role in mobilizing the fatty acids in the fish.

In mammals the catecholamines stimulate the decomposition of triglycerides in the adipose tissue by increasing the formation of cyclic 3'5' AMP. The hormones act on the adenyl cyclase which is responsible for the formation of the cyclic nucleotide. It seems proved that there is a correlation between intracellular level of cyclic 3'5' AMP and the production of free fatty acids in the adipose tissue (WEISS et al. 1966). The catecholamines stimulate the decomposition of the glycogen in the liver of mammals through a practically similar mechanism; the only difference is that here the cyclic 3'5' AMP exerts an influence on the phosphorylase kinase enzyme, and, through this, on the

phosphorylase. From the fact that the blood glucose level in the fish has increased after administration of catecholamines, it can be concluded that the catecholamine stimulated decomposition of glycogen in the liver of the fish occurs similarly to that in mammals, with other words in the liver of the fish, too, there is a biochemical system, consisting of an adenyl cyclase-3'5' AMP-cyclic nucleotide-sensitive enzyme (phosphorylase). On the other hand, from the ineffectiveness of norepinephrine in stimulating the lipolytic processes in fish adipose tissue might be inferred that this system is partly or entirely absent in the adipose tissue of fish.

In connection with the above, it is tempting to assume that there is a relationship between the innervation of the adipose tissue and the presence of the adrenerg lipolytic system in it. According to several authors, in the adipose tissue of the mammals the adipose cells are in connection with nervefibres (HAUSBERGER 1934, BOEKE 1933), and recently, GOVIRIN and POPOVA (1965) have demonstrated in rat adipose tissue in contrast to WIRSEN (1964) a three-dimensional adrenerg network surrounding the adipose cells. It is interesting that in the adipose tissue of lower vertebrates these structures could not be detected, adrenerg structures were found only in connection of blood-vessels (GOVIRIN and POPOVA 1965). This hypothesis is also supported by the fact that in most tissues in which there exists some adrenerg biochemical system (phosphorylase), the cells are in connection with sympathetic fibres (liver). Thus, both the innervation of the adipose tissue and the appearance of the adrenerg lipolytic system in the adipose cells, might be a stage in the evolution of control of lipid metabolism.

The mechanism itself through which norepinephrine decreases the free fatty acid level in fish adipose tissue and blood plasma is not yet clear. The assumption that the hormone inhibits directly the lipolytic processes in the adipose tissue, might be excluded on the basis of analytical data obtained on the glycerol level of blood plasma. From the fact that the plasma glycerol level has not changed significantly after injection of norepinephrine, it can be concluded that the decomposition of triglycerides was continuing, with unchanged intensity in the adipose tissue of the treated animals. It seems to be more probable that the "antilipolytic" effect of the hormone is due to its hyperglycaemic action. Norepinephrine and even stress conditions affected the plasma free fatty acid level as if the animals had been treated with glucose. Glucose, on the other hand, increases the intensity of the re-esterification of the liberated fatty acids in the adipose tissue. The uptake of glucose and the re-esterification of fatty acids are also stimulated by catecholamines in the adipose tissue of mammals (VAUGHAN 1961, CAHILL et al. 1960). Thus, the decrease of plasma and adipose tissue free fatty acid level obtained by the effect of norepinephrine, might be the result of a more intensive re-esterification. In mammals, however, this action of norepinephrine is less evident because of slight glycaemic and strong lipolytic effect — in fish however it might be much more conspicuous because of the lack of the adrenerg lipolytic system.

Summary

Noradrenaline in vivo (2 mg) did not increase the free fatty acid level in the blood of different freshwater fish species (carp, bream and pike-perch). The blood glucose level was increased and the plasma free fatty acid level

decreased after the administration of the hormone. The hormone did not stimulate, even under in vitro conditions (2 μg/ml) the decomposition of triglycerides in the adipose tissue of different fishes (carp, bream, pike-perch, perch, shad). Under its influence the free fatty acid production of the adipose tissue in animals collected in winter, decreased while those of animals collected in summer, did not change. Under stress conditions (cold stress, injection of physiological solution, anoxia) the blood glucose level was increased, however, the plasma free fatty acid level either remained unchanged or decreased (carp, pike-perch, bream). The "antilipolytic" effect of the hormone might be in relation to its hyperglycaemic effect. It is supposed that, in fishes in contrast to mammals the sympathetic nervous system, has no role in mobilizing the fats in the form of free fatty acids.

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VIZSGÁLATOK ÉDESVÍZI HALAK ZSÍRANYAG FORGALMÁN. SZIMPATIKUS IDEGRENDSZER ÉS ZSÍRMOZGÓSÍTÁS

Farkas Tibor

Összefoglalás

Noradrenalin in vivo (2 mg) nem növelte különböző édesvízi halak (ponty, dévér, süllő) vérének szabad zsírsav szintjét. Hatására emelkedett a vércukor szint, és csökkent a plazma szabad zsírsav szintje. A hormon in vitro körülmények (2 μg/ml) között sem stimulálja a trigliceridek lebontását hal (ponty, dévér, süllő, sügér, garda) zsírszövetében. Hatására a télen gyűjtött állatok zsírszövetének szabad zsírsav termelése csökkent, a nyáron gyűjtötteké nem változott. Stress állapotok (coldstress, egyszerű deszt. víz. injekció, anoxia) hatására növekedett a vércukor szint, de a plazma szabad zsírsav szint változatlan maradt, vagy csökkent (ponty, süllő, dévér). A hormon „antilipolitikus" hatását hiperglikémiás hatásával lehet összefüggésbe hozni. Valószínűnek látszik, hogy a szimpatikus idegrendszer az emlősökkel ellentétben halaknál nem játszik szerepet a zsírok szabad zsírsavak formájában történő mozgósításában.

ИССЛЕДОВАНИЕ ОБМЕНА ЖИРОВ ПРЕСНОВОДНЫХ РЫБ. СИМПАТИЧЕСКАЯ НЕРВНАЯ СИСТЕМА И МОБИЛИЗАЦИЯ ЖИРА

Тибор Фаркаш

Норадреналин (2 мг) in vivo не повышает уровня свободных жирных кислот в крови некоторых пресноводных рыб (карп, лещ, судак). Под его влиянием повышается уровень сахара в крови и понижается содержание свободных жирных кислот в сыворотке. Этот гормон (2 μг) in vitro тоже не увеличивает распад триглицеридов в жировой ткани рыб (карп, лещ, судак, окунь, чехонь). Под влиянием норадреналина у животных, собранных зимой, понижается синтез свободных жирных кислот, а у животных, собранных летом—остается без изменения. При шоковых состояниях (холодовой шок, введение дистиллированной воды, аноксия) увеличивается уровень сахара в крови, но содержание свободных жирных кислот в сыворотке остается без изменения или незначительно снижается у карпа, леща и судака. Антилиполитическое действие гормона связано его гипергликемическим воздействием. По всей вероятности, симпатическая нервная система у рыб в отличие от млекопитающихя не играет роли в мобилизации жиров и в виде свободных жирных кислот.