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The effect of a high-fat diet on redox homeostasis indicators and nonspecific immunity in rats*

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ABSTRACT

Growing Wistar rats (30 animals) were divided into 3 groups of 10 each and fed semisynthetic diets: control (C), high-fat (67%) containing soyabean oil (O) or lard (L). After 5 weeks the animals were anesthetized and blood was sampled for analysis of nonspecific immunity indicators, antioxidant enzymatic activity, and blood count. Diet L (lard) led to increased activity of stimulated neutrophils and monocytes. The oxidative burst of neutrophils, activated by *E. coli,* was stimulated by the consumption of an energy-dense diet (lard and oil vs control), whereas the number of phagocytosing cells with reactive oxygen species was smaller in the group of animals fed lard. Moreover, disorders of redox homeostasis were found; diminished superoxide dismutase activity was accompanied by increased GPx activity in rats receiving a high level of dietary fat.

KEY WORDS: rats, lard, soyabean oil, phagocytosis, neutrophils, antioxidant enzymes

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INTRODUCTION

Diet composition can considerably modify some metabolic mechanisms. Extreme diets, which include carbohydrate-free diets (unlimited fat), can cause significant subclinical changes leading to many diseases, but they can also show favourable pharmacological effects. Changes in the amount and quality of consumed nutrients, especially fat, should be made on the basis of a comprehensive evaluation of the impact of such a diet on health.

Changes in the chemical composition of the diet can affect the body's immune system (Chandra and Sarchielli, 1993) and redox homeostasis (Sies, 1985), affecting as a result the health and longevity of humans and animals (Sohal, 1993). A diet that alters the balance between radical-generating and radical scavenging systems may lead to the predominance of reactive oxygen species (ROS) formation and be the cause of numerous diseases. Stimulation of phagocytosing cells also leads to the release of excessive amounts of lethal species (including ROS). ROS released by activated neutrophils can lead to tissue degradation and DNA mutations in cells located close to neutrophils (Weitzman et al., 1985; Dugas et al., 1995).

Polyunsaturated fatty acids (PUFA), the n-6 or n-3 series, can modify the body's immune responses in diverse ways. Fat quality is another factor modifying oxidative stress. Oxidative stress is, however, also related to the intensity of respiration in the mitochondrial respiratory chain and can depend to a large extent on feeding intensity. A key problem seems to be the yet imperfectly understood signaling role of ROS (Cord, 2000) and the interaction between ROS arising through oxidation in the mitochondrial respiratory chain and those synthesized in the process of activating phagocytic cells.

The objective of this study was to determine the effect of a diet with an extremely high fat content provided by soyabean oil or lard, on nonspecific immune status and on selected markers of the redox state in growing rats.

MATERIAL AND METHODS

Growing male (30 animals) were divided into 3 groups of 10 animals each and housed in individual cages for 5 weeks. The animals were maintained under standard conditions: temperature, 21ºC; humidity, 60%; lighting, day/night 12/12 h. The rats were weighed once a week, their health was assessed daily. The animals had free access to water and feed. The control feed (C) was formulated in compliance with NRC requirements (1985), feeds (O) and (L) did not contain starch, but had an increased content of soyabean oil (O) or lard (L) (Table 1). The fatty acid composition of soyabean oil and lard is presented in Table 2.

TABLE 1

Components and chemical composition of the experimental feeds, %

Component	Group		
	control	soyabean oil	lard
Casein	14.5	24.5	24.5
Maize starch	73.2	-	-
Cellulose	3.2	3.2	3.2
Soyabean oil	4.0	67.1	-
Lard	-	-	67.1
DL-Methionine	0.12	0.20	0.20
Mineral mixture[1]	3.0	3.0	3.0
Vitamin mixture[2]	2.0	2.0	2.0

[1] composition of mineral mixture (g/1 kg): $CaHPO_4$ 705.0; K_2HPO_4 81.0; K_2SO_4 68.0; NaCl 30.6; $CaCO_3$ 21.0; Na_2HPO_4 21.5; MgO 25.0; ferrous citrate 5.58; $ZnCO_3$ 30.81; $MnCO_3$ 4.21; $CuCO_3$ 0.23; KJ 0.01; citric acid 7.06

[2] composition of vitamin mixture (mg/1 kg): vit. A 20000 IU; vit. D3 2000 IU; vit. E 100 IU; mg: vit. K 5; choline 200; paraaminobenzoesic acid 100; inositol 100; niacin 40; riboflavin 8, thiamin 5; pyridoxine 5; folic acid 2; biotin 0.4; vit. B_{12} 0.03

TABLE 2

Proportion of fatty acid to the total fatty acids pull, %

Fatty acid	Soyabean oil	Lard
14:0	1.2	1.6
16:0	11.8	23.7
16:1n-7	0.1	2.9
18:0	4.2	12.7
18:1n-9	23.4	47.8
18:2n-6	52.6	7.5
18:3n-3	6.4	0.4
20:0		0.2
20:1n-9		1.3
20:2 n-6		0.4
20:4 n-6		0.6
22:5 n-3		0.1
22:6 n-3		0.1

At the end of the experiment the animals were fasted for 12 h and then anesthetized (ketamine, intramuscularly at a dose of 50 mg/kg BW) and blood was sampled from the heart. The rats were euthanised with an overdose of ketamine. Blood and serum were processed in keeping with standard procedures for determination of particular parameters.

Nonspecific immune indicators were assayed in whole blood sampled into heparinized tubes. The phagocytic activity of monocytes and neutrophils stimulated by *E. coli* and the oxidative burst stimulated by *E. coli*, fMLP (N-formyl-

Met-Leu-Phe) and PMA (phorbol 12-myristate 13-acetate) were studied using Phagotest, Bursttest (Orpegen Pharma, Heidelberg, Germany), and flow cytometry (FACStrak, Becton Dickinson, Belgium).

Antioxidation indicators were investigated by measurement of total antioxidant status (TAS), superoxide dismutase (SOD) and glutathione peroxidase (GPx) activities using Randox Laboratories Ltd. kits at 37ºC in a COBAS FARA II analyser at a wave length of 600 nm for TAS activity, 500 nm for SOD activity, and 340 nm for GPx activity (McCusker et al., 1993; Smart et al., 1993). TAS was determined in serum, whereas SOD and GPx activity, in erythrocytes of blood sampled into tubes containing EDTA-2K and lysed with water.

Blood morphology was determined using standard methods and a Danam-510 analyser (France). Fatty acids were assayed by standard methods (PN-EN ISO 5508, 1996) using a Hewlett Packard-1580 GC from SGE Inc. Austin. with a FID on a 50 m capillary BPX 70 column. The peaks were identified using standards (Promochem), amounts were expressed in percent of total fatty acids.

The results were subjected to statistical analysis by monofactorial ANOVA and Duncan's range test, using the Statgraphic 4.1 Plus software package.

RESULTS

Feeding high-fat, starch-free diets to rats did not significantly affect the percent of neutrophils or monocytes phagocytosing *E. coli* (Table 3). An increase was, however, found in fluorescence intensity, expressed in fluorescence units (FU), of both neutrophils and monocytes in the blood of rats that had received lard, in comparison with the other groups of animals. Fluorescence intensity determined by flow cytometry was a measure of the number of *E. coli* cells phagocytosed by the particular cells. It was found that the largest difference (about 30%) in phagocytosis intensity of both neutrophiles and monocytes was between the groups of rats fed soyabean oil (lowest) and lard (highest).

TABLE 3

Phagocytic activity of neutrophils and monocytes in peripheral blood of control and experimental rats

Cell	Parameters	Groups			SE pooled	P
		control	oil	lard		
Neutrophils	Percent of phagocytosing cells	86.7	88.0	89.3	2.653	0.1124
	Mean fluorescence intensity - FU[1]	762^a	643^a	963^b	32.42	0.0238
Monocytes	Percent of phagocytosing cells	84.7	68.0	82.0	4.425	0.0894
	Mean fluorescence intensity - FU[1]	498^a	441^a	610^b	14.84	0.0317

FU[1]- fluorescence units (4 decades, 1025 channels, log)

[a,b] significant difference at P<0.05

The study also investigated the effect of the diet on the intensity of the respiratory burst of neutrophils phagocytosing cells stimulated by *E. coli*, fMLP, and PMA (Table 4). Stimulation by fMLP and PMA showed the lowest percentage of cells killing by the use of reactive oxygen species (ROS) in rats fed the diet containing lard. The intensity of the *E. coli*-stimulated oxidative burst measured by determination of fluorescence intensity in ROS-producing cells was higher in the animals fed the experimental diets. Stimulation by fMLP increased the intensity of the oxidative burst of rats fed the soyabean oil-containing diet.

TABLE 4

Oxidative burst activity of neutrophils in peripheral blood of control and experimental rats

Activators	Parameters	Groups			SE pooled	P
		control	oil	lard		
E. coli	Oxidizing cells, %	94	92	86	2.581	0.1104
	Mean fluorescence intensity, FU[3]	24.01^{a}	38.55^{b}	32.45^{b}	2.223	0.0007
fMLP[1]	Oxidizing cells, %	94^{a}	93^{a}	85^{b}	2.062	0.0173
	Mean fluorescence intensity, FU[3]	2.46^{a}	5.19^{b}	3.76	0.523	0.0105
PMA[2]	Oxidizing cells, %	85	92^{a}	83^{b}	2.667	0.0755
	Mean fluorescence intensity, FU[3]	21.26	13.24	11.62	8.945	0.4847

[1] fMLP - N-formyl-Met-Leu-Phe; [2] PMA - phorbol 12-myristate 13-acetate; FU[3]- fluorescence units (4 decades. 1025 channels. log)

[a,b] significant difference at P<0.05

The results of this experiment show that the activity of superoxide dismutase in the erythrocytes of rats was smaller in the experimental groups, although in rats fed the "high-oil" diet, it did not reach statistical significance (Table 5). In contrast, glutathione peroxidase activity showed the opposite tendency and was higher in the blood of rats fed the "high-lard" diet. Blood morphology of rats given the experimental diets (groups O and L) showed a higher erythrocyte count and haemoglobin concentration (Table 6). No differences in the white blood cell profile were found.

TABLE 5

Activity of antioxidative enzymes (U/l) in peripheral blood of control and experimental rats

Enzymes	Groups			SE pooled	P
	Control	Oil	Lard		
Total antioxidant status	0.88	0.97	0.92	0.0712	0.1820
Superoxide dismutase	2.04^{a}	1.56	1.49^{b}	0.1441	0.0134
Glutathione peroxidase	246^{a}	271	282^{b}	10.04	0.0459

[a.b] significant difference at P<0.05

TABLE 6

Haematological parameters in peripheral blood of control and experimental rats

Parameters	Groups			ANOVA	
	control	oil	lard	SE pooled	P
White blood cell, G/l	5.5	5.2	6.2	0.738	0.7300
Red blood cell, T/l	6.5[ac]	7.3[bd]	7.1[b]	0.1446	0.0017
Mean corpuscular volume, fl	58	53	54	0.9739	0.0652
Hemoglobin, g/l	129[ac]	137[b]	139[bd]	2.167	0.0109
Hematocrit, l/l	0.37	0.39	0.39	0.0079	0.1580

[ab, cd] significant difference at $P<0.05$

DISCUSSION

Neutrophils are the most numerous population of phagocytosing cells. This activity is supplemented by the much less numerous monocytes and by macrophages in tissues. The efficiency of phagocytosing cells depends on numerous factors, among which the important ones include chemotaxis and the ability to synthesize toxic compounds enabling the destruction of a foreign body. The killing mechanisms can be divided into oxidative, involving toxic compounds of oxygen and their oxygenated halides, and non-oxidative mechanisms. Proteins found in the azurophil and specific granules are the main element of non-oxidative mechanisms of eliminating foreign bodies (Jakóbisiak, 2000). Killing mechanisms (both chemotaxic and production and secretion of toxic substances) begin with the activation of the immune system by various factors, including bacterial cells and some chemical compounds. The factors activating phagocytosing cells include the stimulators used in this study, fMLP, PMA, as well as other nonbacterial factors, arachidonic acid (AA), leukotrien B_4 (LTB_4), tumor necrosis factor (TNF), and Ca^{2+} ionophores (Hampton et al., 1998). The most effective chemotactic factors in respect to neutrophils and monocytes include C5a, LTB_4, fMLP and some cytokines released by phagocytes, IL-1, TNF-α, TGF-β, IL-8 (Clark, 1999). The migration of phagocytes in the direction of the chemotactic factor makes it possible to achieve the goal, but the efficiency of the cytotoxic response is affected by the activation of the phagocytes. IL-8 plays a decisive role in activation of neutrophils. Proinflammatory cytokines, including IL-1, IL-2, TNF-α, and IFN-γ, stimulate the release of chemokines, whereas TGF-β, IL-4, and IL-10 inhibit their release (Clark, 1999). In the stimulated phagocyte, enzymes responsible for the synthesis of both oxidative and non-oxidative cytotoxic compounds are expressed.

Metabolic processes in activated cells and their chemotoxic abilities can depend on the presence in the cell of chemical compounds that are available for metabolic processes. Cell membrane phospholipids are a storehouse of fatty acids needed in cellular metabolism. The composition of phospholipids depends, among others, on the diet (Kotkat et al., 1999). The diets used in this study differed in the source of fat, and therefore, in their fatty acid content. The high-oil diet containing soyabean oil was a source, of, among others, linoleic acid-precursor of arachidonic acid C20:4n-6 (AA) and, to a lesser degree, of α-linolenic acid - precursor of eicosapentaenoic acid C20:5n-3 (EPA) (Sawosz et al., 1999). Twenty-carbon PUFA are a source of ecosanoids, but the type of eicosanoids synthesized depends on the series of fatty acids from which they are derived. The acids contained in the soyabean oil used in this study could have been the source of both proinflammatory ecosanoids (LTB4) and anti-inflammatory ones (PGE3 and LTB5). Lard is also a source of unsaturated fatty acids. Dietary fats usually show a tendency to occupy a certain position in the consecutive carbons of glycerides. The triacylglycerides (TAG) of lard usually contain a C16:0 acid at carbon sn-2 (Brockerhoff, 1966), and an unsaturated fatty acid at carbon sn-1,3. This makes lard a very effective source of AA despite being a relatively poor source of the precursor of AA, linoleic acid, in comparison with soyabean oil.

In summary, it can be accepted on the basis of earlier studies (Sawosz, 1999) and the available literature, that adding soyabean oil to the diet leads to the enrichment of tissue lipids in linoleic and α-linolenic acids, while adding lard, in arachidonic acid.

Analysis of the effect of the diets on phagocytic activity of neutrophils and monocytes shows a significant increase in phagocytic activity with the use of non-oxidative factors in response to the addition of lard to the diet of rats (Table 2). Increased killing cell activity was caused by the activation and acceleration of chemotaxis. Lard is a source of linoleic acid and of arachidonic acid, which in turn is a precursor of LTB_4. It may, therefore, be presumed that the increased phagocytic activity of neutrophils and monocytes stimulated by *E. coli* observed in this experiment may have additionally been activated by secretion of AA stored in cellular phospholipid structures and which became a source of LTB_4. Leukotriene B_4 exhibits strong chemotactic activity.

In the presented experiment, no inhibitory effect of soyabean oil was found on the phagocytic activity of neutrophils. Studies on the use of various types of oil (coconut, olive, safflower, evening primrose, menhaden) also failed to show that they differentiated subpopulations of lymphocytes, affected the ratio of lymphocytes to macrophages, NK cells, and expression of adhesion molecules (LFA-1, ICAM, CD2) (Yaqoob et al., 1995). In other studies, it was found that EPA given to rats reduced the synthesis of IL-1, IL-2, IL-6, TNF-α, IFN-γ by mononuclear peripheral blood cells (Calder, 1998). Seya et al. (1988) observed that long-chain PUFA n-3, administered to humans, reduced chemotaxis of neutrophils and monocytes by inhibiting the outflow of calcium ions as the result of the arachidonic acid cascade. Moreover, it was shown that EPA contained in fish oil inhibits proliferation of T lymphocytes and the production of interleukins (Calder et al., 1992). In the presented experiment, a significant effect on reducing the phagocytic activity of cells as the result of including soyabean oil in the diet for rats was not observed. Although soyabean oil is also a source of α-linolenic acid and, indirectly, of EPA, although neutrophil activity in the group of rats fed soyabean oil was the lowest.

It can, therefore, be assumed that in the studied rats, the differentiated phagocytic activity of neutrophils (lard vs control, oil) involving non-oxidative mechanisms was caused by the provision of lard in the diet and the probable increase in the amount of AA deposited in the phospholipids of the cellular membranes of immune system cells.

Activated phagocytes react with the oxidative mechanism of killing foreign cells and bodies, which is often referred to as a oxidative burst of phagocytosing cells. This mechanism is based on the activation of NADPH oxidase that is a part of the cytochrome b558 protein chain that transports electrons to oxygen. This process leads to the formation of the superoxide radical, O_2^-, and then, as the result of spontaneous dismutation, to hydrogen peroxide and, presumably through the Fenton reaction, to the hydroxyl radical ^-OH, as well as oxidated halides and other ROS. In addition to oxidative bursts, ROS also arise in the mitochondrial respiratory chain in amounts proportional to the intensity of oxygen utilization and metabolism (Sohal et al., 1995; Chandra and Sarchielli, 1996).

In this experiment we observed an increase in oxygen-depend killing activity (stimulated by *E. coli* and fMLP) in the neutrophils of rats given a high-fat diet, regardless of the type of fat (Table 3). Regardless then of the source of fat (oil or lard), the amount of ROS in cells increased. It can be supposed that rats that consumed a more energy-dense diet were characterized by more intensive metabolism in the mitochondrial respiratory chain. The process of electron transfer in the mitochondrial respiratory enzyme chain is accompanied by the release of a certain amount of ROS, which can increase as the intensity of oxidation increases in the mitochondrial chain (Cutler, 1991) or decrease during feeding restriction (Weindruch R., 2002). The interaction of ROS - by-products of electron transport in the mitochondrial chain of respiratory proteins and the enzymes generating ROS for the destruction of invading microorganisms in phagocytosing cells is unknown.

The experiment showed that in the neutrophils of rats fed lard, the number of cells killing with ROS was significantly smaller in comparison with the control group and with the group fed the high-oil diet. Soyabean oil is a source of C18:2n-6 acid, but also of C18:3n-3 (and further in tissues, of EPA), which act as TNF-α inhibitors. TNF-α influences the cellular redox potential (Schreck et al., 1991) regulating apoptosis and cell proliferation. It has been shown that TNF increases the release of O_2^- by stimulating phagocytosing cells in the blood (Ward et al., 2000). As a proinflammatory cytokine, TNF-α is inhibited by EPA and stimulated by AA (deposited as the result of the supply of lard in the diet). It can therefore be presumed that AA (maybe through TNF-α) decreases the number of neutrophils killing with the use of ROS. It cannot be excluded that in this case, the pathway AA → TNF-α → ROS → led to the reduction of the number of phagocytosing cells. Garg and Aggarwal (2002) point to the key role of ROS in TNF signaling.

The fact that ROS are generated by an energy-dense diet regardless of the source of fat is supported by the SOD activity observed in the experiment (Table 4). Rats receiving a diet rich in fat were characterized by a lower SOD concentration in erythrocytes, which may have been the result of the involvement of the enzyme in dismutase reactions with the superoxide anion O_2^- arising in excessive amounts. The superoxide anion undergoes dismutation to hydrogen peroxide, which in turn is degraded by glutathione peroxidase (GPx) as well as by catalase. In the experiment we observed higher GPx concentrations in rats fed the experimental diets than in the controls. It thus seems that the process of degrading excess H_2O_2 was effective. O_2^- may undergo spontaneous dismutation or dismutation with the participation of SOD. Spontaneous dismutation of O_2^- causes a sudden decrease in the concentration of superoxide and increase in the amount of H_2O_2, dismutation with the participation of SOD, however, makes it possible to maintain a steady level of superoxide (Babior, 2000). The lower SOD activity may result from the extensive involvement of SOD in reactions with O_2^-, which made the gradual production of H_2O_2 and its effective oxidation by GPx possible.

CONCLUSIONS

It seems that a mechanism can be considered in which the phagocytic activity of neutrophils and monocytes is stimulated by the diet. A high-fat diet containing lard may significantly increase the activity of stimulated cells, neutrophils and monocytes. This state may favour the cytotoxic activity of phagocytosing cells directed against the body's own tissues. The oxidative burst of neutrophils activated by *E. coli* is probably stimulated by the consumption of an energy-dense diet. Consumption of such a diet is associated with increased electron transportation in the mitochondrial respiratory chain and proportionately greater production of ROS and therefore the greater involvement of SOD in scavenging O_2^-, which is suggested by the results of this study. By excessive activation of neutrophil oxidative bursts, an energy-dense diet may lead to an imbalance in redox homeostasis. It seems, however, that consuming a diet containing a large amount of lard is particularly unfavourable, since on the one hand, excessive activation of cells phagocytosing through oxidative and non-oxidative mechanisms (monocytes and neutrophils) can be observed, while on the other hand, the number of phagocytosing neutrophils undergoes a significant reduction, which may point to a certain degree of immunosuppression.

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STRESZCZENIE

Wpływ diety wysokotłuszczowej na wskaźniki równowagi antyoksydacyjnej i stanu odporności nieswoistej u szczurów

Rosnące szczury rasy Wistar (30 sztuk) podzielono na 3 grupy po 10 i żywiono mieszankami półsyntetycznymi: kontrolną (I), wysokotłuszczową (67% mieszanki) z udziałem oleju sojowego (II) lub smalcu (III). Po 5 tygodniach zwierzęta poddano narkozie i pobrano krew do analiz. We krwi oznaczono wskaźniki odporności nieswoistej, aktywność enzymów antyoksydacyjnych oraz wskaźniki morfologiczne. Podawanie diety III (smalec) spowodowało zwiększenie aktywności komórek stymulowanych neutrofili i monocytów. Wybuch tlenowy neutrofili, aktywizowany *E. coli*, był stymulowany pobraniem diety o wysokiej koncentracji energii (smalec i olej vs kontrola), natomiast liczba komórek fagocytujących z udziałem ROS była mniejsza w grupie zwierząt otrzymujących smalec. Stwierdzono ponadto zakłócenie równowagi redox poprzez zmniejszenie aktywności SOD, jednocześnie zwiększenie aktywności GPx u szczurów otrzymujących diety o dużej zawartości tłuszczu.