Effect of Dietary Oils on Lymphocyte Immunological Activity in Psychologically Stressed Mice

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Psychological stress has been shown to modulate immune functions. In this study, we investigated the effect of dietary oils (olive oil, soybean oil, and fish oil) on the social isolation stress-induced modulation of lymphocyte immunological activities in mice. In olive oil-fed, but not soybean oil- or fish oil-fed, mice, a 2-week isolation stress decreased the lymphocyte proliferative response, reduced the interferon-γ and interleukin (IL)-10 secretions and increased the IL-4 secretion by lymphocytes. The isolation stress reduced the arachidonic acid content of lymphocytes markedly, moderately, and not at all in the olive oil-, soybean oil-, and fish oil-fed mice, respectively. In the olive oil-fed, but not soybean oil- or fish oil-fed, mice, the isolation stress up-regulated the expression level of mRNA for splenic heat-shock protein 70 and increased lymphocyte sensitivity to the antiproliferative effect of corticosterone. This is the first demonstration that effect of psychological stress on lymphocyte immunological activities can vary depending upon the dietary fatty acid composition.

Key words: arachidonic acid (AA) content; dietary fish oil; dietary olive oil; lymphocyte immunological activity; social isolation stress

A growing body of evidence indicates that psychological stress is responsible for modulation of immune functions and increases the susceptibility to and severity of inflammatory and infectious diseases.1–3) Elderly caregivers have shown impairment in T cell proliferation and natural killer (NK) cell number and activity, and elevation in the herpes virus antibody titer.4,5) Social isolation of laboratory animals is used as a model to study the behavioral, neurochemical and immunological consequences of the absence of social interaction in rodents.6) Social isolation stress decreases NK cell activity and enhances the metastasis of transplantable tumours in mice.7)

It is well known that the alteration of fatty acid composition in immunocompetent cells is associated with modulation of such immunological functions as lymphocyte proliferation, cytokine production, and NK cell activity.8,9) The fatty acid composition of immunocompetent cells is altered according to the fatty acid composition of the diet10,11) and this leads to a change in these cells to produce the eicosanoids which are involved in immunoregulation.12) It has been reported that academic examination stress (psychological stress) was responsible for the reduction of plasma arachidonic acid (20:4n-6; AA) content in humans.13) Injecting rats with dexamethasone (the corticosteroid hormone) de-
increased the AA content and increased the oleic acid (18:1n-9; OA) and linoleic acid (18:2n-6; LA) contents in hepatic microsomal total lipids. These findings suggest that psychological stress-induced modulation in the immune functions would, at least partly, be due to an alteration in the fatty acid composition of immunocompetent cells. We thus hypothesized that dietary supplementation with certain oils or fatty acids could modulate the physiological effects of psychological stress on immune functions. In an attempt to elucidate whether dietary oils with different fatty acid compositions could differently modulate the psychological stress-induced alteration of immune functions, we investigated the effect of three dietary oils (olive oil, soybean oil, and fish oil) on the fatty acid composition and immunological activities of lymphocytes under psychological stress (social isolation) in mice.

Materials and Methods

Diets. The experimental diets were designed according to the AIN-76A diet guidelines, with minor modifications necessary to accommodate an increase in caloric density as the fat content was increased from 5% to 15% by weight. Casein, α-corn starch, sucrose, cellulose powder, AIN-76A mineral mixture, AIN-76A vitamin mixture and choline bitartrate were purchased from Oriental Yeast (Tokyo, Japan). DL-methionine was obtained from Wako Pure Chemical Ind. (Osaka, Japan). Olive oil, soybean oil and fish oil were kindly supplied by NOF Corporation (Tokyo, Japan). The test diet (in wt. %) consisted of 23.0% casein, 40.4% α-corn starch, 9.7% sucrose, 5.8% cellulose powder, 4.0% AIN-76A mineral mixture, 1.4% AIN-76A vitamin mixture (containing 5 mg/g of dl-α-tocopherol acetate), 0.4% DL-methionine, 0.3% choline bitartrate, and 15.0% test oil. The three diet groups were differentiated by lipid source according to the AIN-76A diet guidelines, with minor modifications necessary to accommodate an increase in caloric density as the fat content was increased from 5% to 15% by weight. The room temperature was kept at 23 ± 1°C. After centrifugation at 3,000 × g for 20 min at 4°C, the serum was flash-frozen in liquid nitrogen and stored at −80°C until extraction.

### Table 1. Fatty Acid Composition of Each Test Oil (g/100g of fatty acid)

<table>
<thead>
<tr>
<th>Fatty acid</th>
<th>Olive oil</th>
<th>Soybean oil</th>
<th>Fish oil</th>
</tr>
</thead>
<tbody>
<tr>
<td>16:0</td>
<td>12.6</td>
<td>17.4</td>
<td>19.2</td>
</tr>
<tr>
<td>16:1(n-9)</td>
<td>1.0</td>
<td>0.1</td>
<td>8.0</td>
</tr>
<tr>
<td>18:0</td>
<td>3.1</td>
<td>5.7</td>
<td>3.8</td>
</tr>
<tr>
<td>18:1(n-9)</td>
<td>75.6</td>
<td>22.3</td>
<td>22.6</td>
</tr>
<tr>
<td>18:1(n-7)</td>
<td>2.2</td>
<td>1.2</td>
<td>3.6</td>
</tr>
<tr>
<td>18:2(n-6)</td>
<td>4.5</td>
<td>46.9</td>
<td>9.0</td>
</tr>
<tr>
<td>18:3(n-3)</td>
<td>0.6</td>
<td>6.1</td>
<td>2.0</td>
</tr>
<tr>
<td>20:1(n-9)</td>
<td>0.2</td>
<td>0.2</td>
<td>1.9</td>
</tr>
<tr>
<td>20:2(n-6)</td>
<td>0.0</td>
<td>0.0</td>
<td>0.3</td>
</tr>
<tr>
<td>20:3(n-6)</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
</tr>
<tr>
<td>20:4(n-6)</td>
<td>0.1</td>
<td>0.0</td>
<td>2.2</td>
</tr>
<tr>
<td>20:5(n-3)</td>
<td>0.0</td>
<td>0.0</td>
<td>7.7</td>
</tr>
<tr>
<td>22:5(n-6)</td>
<td>0.1</td>
<td>0.0</td>
<td>0.0</td>
</tr>
<tr>
<td>22:5(n-3)</td>
<td>0.0</td>
<td>0.1</td>
<td>2.1</td>
</tr>
<tr>
<td>22:6(n-3)</td>
<td>0.0</td>
<td>0.0</td>
<td>17.6</td>
</tr>
<tr>
<td>Total saturated fatty acid</td>
<td>15.7</td>
<td>23.1</td>
<td>23.0</td>
</tr>
<tr>
<td>Total MUFA</td>
<td>79.0</td>
<td>23.8</td>
<td>36.1</td>
</tr>
<tr>
<td>Total n-6 PUFA</td>
<td>4.7</td>
<td>46.9</td>
<td>11.5</td>
</tr>
<tr>
<td>Total n-3 PUFA</td>
<td>0.6</td>
<td>6.2</td>
<td>29.4</td>
</tr>
<tr>
<td>Total n-6 + n-3 PUFA</td>
<td>5.3</td>
<td>53.1</td>
<td>40.9</td>
</tr>
</tbody>
</table>

Detecting the fatty acids detected in the olive oil. The soybean oil has very little docosapentaenoic acid (22:5n-3; 0.1%) and no measurable quantities of any other n-3 PUFAs. In contrast, the n-3 PUFAs in the fish oil consisted mainly of docosahexaenoic acid (22:6n-3; DHA) and eicosapentaenoic acid (20:5n-3; EPA) at 18% and 8% of total fatty acid, respectively. The saturated fatty acids, 16:0 and 18:0, were present in all the test oils and comprised 16–23% of their total fatty acid.

Animals and housing conditions. Specific pathogen-free 4 week-old female BALB/c mice were obtained from Charles River (Atsugi, Japan). The animals were group-housed (4 mice per 32 × 22 × 11 cm2 aluminum cage) and maintained on a standard non-purified diet (Oriental Yeast) and water *ad libitum* for 1 week, before being maintained on a test diet containing 15% olive oil, soybean oil or fish oil and water *ad libitum*. Three weeks after starting the test diet, the mice were either 1) housed under the same conditions (4 mice per 32 × 22 × 11 cm2 aluminum cage; group-housed) or 2) kept individually (1 mouse per 30 × 18 × 11 cm3 aluminum cage; isolated), and maintained on the same test diet and water. In either group, the light cycle was maintained at 12 h on and 12 h off. The room temperature was kept at 23 ± 1°C. After 2 weeks under the housing conditions just specified, the animals were sacrificed by decapitation between 8:00 and 8:30 a.m. Blood was collected and allowed to clot for 1 hour at room temperature. Serum was then separated by centrifugation at 3,000 × g for 20 min at 4°C. Portions of the serum samples were stored at −80°C until needed for an analysis of corticosterone.
needed for the preparation of RNA. The housing, handling and sample collection procedures conformed to the policies and recommendations of the Laboratory Animal Care Advisory Committee of Chiba University.

**Real-time quantitative RT-PCR.** Total RNA was isolated from the spleens by using an RNAeasy extraction kit according to the manufacturer’s directions (Qiagen, Hilden, Germany). cDNA was synthesized from 1 μg of total RNA with oligo-dT primers by using the Reverse Transcription System (Promega, Madison, WI, USA) according to the manufacturer’s instructions. Real-time quantitative RT-PCR analyses were performed in 20 μl of SYBR Green PCR master mix (Applied Biosystems, Foster City, CA, USA) containing 300 nm primers and 5 ng of reverse transcribed total RNA in an ABI PRISM 7000 Sequence Detection System. The primer sequences were used (with abbreviation, product size and GenBank accession number noted in parentheses) heat-shock protein 70 (HSP70, 185 bp, NM_010479) 5'-AAGCGTCACCTCTCTGACCT-3', 5'-TGCTGAATGCTCCTTGTG-3'; ubiquitin C (UBC, 182 bp, BC025894) 5'-GACCAAGAGGGCTGATC-3', 5'-GTGTAACACTGGCTGAC-3'; proteasome subunit beta type 1 (PSMB1, 104 bp, NM_010479) 5'-ACCTCGTAAAGGCAAG-3', 5'-CCACCTGCTGGTACGAC-3'; proteasome subunit C2 (PSM2, 182 bp, AJ272019) 5'-CAATTTGCGGTC-TAATCTG-3', 5'-GAGCAGCCCAACACCATAC-3'; proteasome 26S subunit ATPase 3 (PSMC3, 182 bp, NM_008948) 5'-AAGCTGAGCCAGGACCT-3', 5'-AAGACAATGGCTTCCACCAG-3'; glucocorticoid receptor (GR, 245 bp, NM_001185) 5'-CCCTGGTAACATTGCGGG-3'; cytosolic thioredoxin (IFN)–γ and of interleukin (IL)-4, IL-6 and IL-10 were determined by an ELISA method with a commercial kit (Amersham, Buckinghamshire, UK).

For the cytokine analysis, each culture (100 μl of the cell suspension and 100 μl of the Con A solution) was incubated for 47 h. The cell supernatant was then harvested and frozen at −80 °C until needed for analysis. The concentrations of interferon (IFN)–γ, and of interleukin (IL)-4, IL-6 and IL-10 were determined by an ELISA method with a commercial kit (Amersham, Buckinghamshire, UK).

**Cytokine assay.** The cytokine analysis, each culture (100 μl of the cell suspension and 100 μl of the Con A solution) was incubated for 47 h. The cell supernatant was then harvested and frozen at −80 °C until needed for analysis. The concentrations of interferon (IFN)–γ, and of interleukin (IL)-4, IL-6 and IL-10 were determined by an ELISA method with a commercial kit (Amersham, Buckinghamshire, UK).

**Fatty acid analysis.** The total lipids were extracted from splenic lymphocytes with a mixture of chloroform and methanol (2:1, v/v). Fatty acid methyl esters were prepared by refluxing the total lipid with a 4% HCl–methanol solution and were analyzed with a GC-8A gas chromatograph (Shimadzu, Kyoto, Japan) in a Supelco-wax-10 fused silica capillary column (0.32 mm × 60 m, Supelco, Bellefonte, PA, USA).

**Assay of serum corticosterone.** The serum corticosterone concentration was determined with a radioimmunoassay kit (ICN Biochemical, Costa Mesa, CA, USA). Serum samples were heated to 90 °C for 30 min prior to their analysis to prevent proteolytic interference during the radioimmunoassay incubation. The assay was carried out in duplicate, and the averages of individual data were statistically analyzed.

**Statistical analysis.** Each data value is expressed as the mean and standard deviation for n observations. Comparisons among the three test diet groups under the same housing condition (group-housing or isolation) ...
were evaluated by ANOVA with the SPSS computer programs (SPSS Japan, Tokyo). A Tukey B test were used for post hoc analysis. Comparisons between the group-housed and isolated mice within each test diet group were assessed by the Levene test and unpaired Student’s t-test.

Results

Food intake and weights of the body and spleen
The five-week-feeding test diets had no significant effect on the food intake (results not shown). The isolation stress increased the food intake by the soybean oil-fed mice (mean ± SD: 3.13 ± 0.11 g/mouse/day for the group-housed mice; 4.33 ± 0.26 g/mouse/day for the isolated mice; n = 6/test group) but did not significantly alter in the olive oil- or fish oil-fed mice. Neither the isolation stress nor test diet had any significant effect on the weights of the body and spleen (results not shown).

Fatty acid composition of total lipid in splenic lymphocytes
In the olive oil- or soybean oil-fed mice, a 2-week isolation stress exposure decreased the AA (20:4n-6) and DHA (22:5n-3) contents of splenic lymphocytes (Fig. 1A and B). These decreases were more profound in the olive oil-fed mice than in the soybean oil-fed mice. By contrast, in the fish oil-fed mice, the isolation stress had no significant effect on the AA and DHA contents of the lymphocytes. The isolation stress in the olive oil-fed mice increased the lymphocyte OA (18:1n-9) content (Fig. 1C). In the soybean oil-fed mice, the isolation stress increased the OA and LA (18:2n-6) contents of the lymphocytes (Fig. 1C and D). In all the dietary oil groups, the isolation stress had no significant effect on the other fatty acid contents of the splenic lymphocytes.

Lymphocyte proliferation and cytokine secretion
When olive oil was fed, the 3H-thymidine uptake by activated splenic lymphocytes was less in the isolated mice than in the group-housed mice (Table 2). By contrast, when soybean oil or fish oil was fed, there was no significant difference between the isolated and group-housed mice in the 3H-thymidine uptake by lymphocytes.

Figure 2 shows the effect of each dietary oil on the cytokine secretion by Con A-stimulated lymphocytes. In

![Graphs showing fatty acid composition](https://example.com/graph1.png)

![Graph showing lymphocyte activity](https://example.com/graph2.png)
the olive oil-fed mice, isolation stress decreased the IFN-\( \gamma \), IL-6 and IL-10 secretion and increased the IL-4 secretion by lymphocytes. In the soybean oil- and fish oil-fed mice, isolation stress decreased the IL-6 secretion, but had no significant effect on the IFN-\( \gamma \), IL-4 or IL-10 secretion by lymphocytes. The decrease in IL-6 secretion was more profound in the olive oil-fed mice than in the soybean oil- and fish oil-fed mice.

**Gene expression levels in spleen cells**

HSP70 is a major heat shock/stress response protein.\(^{15}\) When olive oil was fed, the HSP70 mRNA expression level in the spleen of the isolated mice was up-regulated to 1.71-fold above that of the group-housed mice (Fig. 3A). In the soybean oil- and fish oil-fed mice, in contrast, the isolation stress had no significant effect on the level of HSP70 mRNA in the spleen. Ubiquitin, one of the smallest HSPs, is known to target proteins for degradation by the 26S proteasome complex.\(^{16,17}\) In the fish oil-fed, but not olive oil- or soybean oil-fed mice, the isolation stress moderately down-regulated the ubiquitin C (UBC) mRNA expression level in the spleen (Fig. 3B). The isolation stress increased expression levels of mRNA for PSMB1, PSMA1 and PSMC3 (26S proteasome subunits) in the olive oil- and soybean oil-fed, but not fish oil-fed mice (Fig. 3C, D and E). The increases were greater in the olive oil-fed mice than in the soybean oil-fed mice. The isolation stress increased the expression of the glucocorticoid receptor at the

### Table 2. Effect of Each Dietary Oil on the Lymphocyte Proliferative Response

<table>
<thead>
<tr>
<th>Activator</th>
<th>Dietary oil</th>
<th>Housing condition</th>
<th>Mean SD</th>
<th>Mean SD</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Group-housing</td>
<td>Isolation</td>
<td></td>
</tr>
<tr>
<td>Anti-CD3</td>
<td>Olive oil</td>
<td>146,382(^{a}) 6,859</td>
<td>127,255*(^{y}) 4,238</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Soybean oil</td>
<td>146,556(^{a}) 6,775</td>
<td>146,961*(^{x}) 6,823</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Fish oil</td>
<td>115,039(^{a}) 6,101</td>
<td>119,736*(^{y}) 4,050</td>
<td></td>
</tr>
<tr>
<td>ConA</td>
<td>Olive oil</td>
<td>123,824(^{a}) 8,489</td>
<td>106,039*(^{x}) 7,966</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Soybean oil</td>
<td>125,774(^{a}) 6,795</td>
<td>124,246*(^{y}) 4,686</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Fish oil</td>
<td>87,153(^{a}) 7,272</td>
<td>88,583(^{a}) 6,670</td>
<td></td>
</tr>
<tr>
<td>LPS</td>
<td>Olive oil</td>
<td>89,635(^{a}) 4,057</td>
<td>76,442*(^{y}) 4,237</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Soybean oil</td>
<td>91,887(^{a}) 6,408</td>
<td>102,011*(^{y}) 4,317</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Fish oil</td>
<td>62,013(^{a}) 4,437</td>
<td>62,128(^{a}) 5,083</td>
<td></td>
</tr>
</tbody>
</table>

Each value is the mean ± SD (n = 4/test group). Mean values with unlike superscript letters (a, b, group-housing; x, y, z, isolation) within the same activator are significantly different (\( P < 0.05 \)). \(^{*}P < 0.05, \text{vs. group-housed mice within each dietary oil group.}\)

### Fig. 2. Effects of Dietary Oils on the Lymphocyte Secretion of Interferon (IFN)-\( \gamma \) (A), and Interleukin (IL)-4 (B), IL-6 (C) and IL-10 (D).

Each value represents the mean ± SD (n = 4/test group). \(*P < 0.05, \text{**}P < 0.005, \text{***}P < 0.0005, \text{significantly different between the group-housed and isolated mice within each test diet group. Values with unlike superscript letters (a, b, c, group-housing; x, y, z, isolation) are significantly different (P < 0.05).}\)
mRNA level in the olive oil- and soybean oil-fed, but not fish oil-fed mice (Fig. 3F).

Serum corticosterone concentration
Under the group-housing condition, the 5-week feeding test diets had no significant effect on the serum corticosterone concentration (mean ± SD: 56 ± 10 ng/ml for the olive oil group; 49 ± 13 ng/ml for the soybean oil group; 53 ± 3 ng/ml for the fish oil group; n = 6/test group). In the fish oil-fed mice, the isolation...
Discussed the effects of dietary oils on lymphocyte sensitivity to the antiproliferative effect of corticosterone. olive oil-fed mice showed significantly reduced lymphocyte sensitivity to corticosterone compared to fish oil-fed mice when stimulated with concanavalin A. Discussion focuses on the link between stress and immune response, with particular emphasis on how different oils affect corticosterone levels and lymphocyte proliferation. The present study showed that olive oil reduced corticosterone levels and increased lymphocyte sensitivity, whereas fish oil had the opposite effect. These findings highlight the importance of dietary oils in modulating the immune response to stress.
ences in tissue and cell sensitivity to glucocorticoid action.\textsuperscript{19} Thus, in the olive oil-fed mice, the isolation stress-induced increase in lymphocyte sensitivity to corticosterone action may be, at least partly, attributable to the enhanced expression of GR (Fig. 3F).

It has been well documented that an alteration in the fatty acid composition of immunocompetent cells is often accompanied with modulation of their immunological functions.\textsuperscript{9,20} The decrease in AA content of immunocompetent cells is accompanied by reductions in the lymphocyte proliferative response, inflammatory cytokine production and NK cell activity.\textsuperscript{11,21} Thus, in the olive oil-fed mice, the isolation stress-induced reduction in the lymphocyte proliferative response and IFN-\(\gamma\) secretion from lymphocytes may have been, at least partly, due to the decrease in AA content of the lymphocytes. On the other hand, under the isolation stress, the Con A- or LPS-stimulated lymphocyte proliferative response was still greater in the olive oil-fed mice than in the fish oil-fed mice (Table 2), while there was no significant difference in the lymphocyte AA content between the former and the latter mice (Fig. 1A). It has been reported that an increase in DHA content not accompanied by any change of AA content in human T cells was responsible for the suppression of IL-2 receptor signaling which is involved in T cell proliferation.\textsuperscript{22,23} Thus, the lower DHA content of lymphocytes in the olive oil-fed mice than in the fish oil-fed mice may, at least partly, account for the greater lymphocyte proliferation in the former mice than the latter.

It is well known that the expression level of mRNA for HSP70 is up-regulated in response to a variety of stress.\textsuperscript{24,25} Exposure to the emotional responses of footshock-stressed rats such as jumping and screaming (a model of psychological stress) increased the level of HSP70 mRNA in the rat aorta.\textsuperscript{26} In the present study, the olive oil-fed, but not fish oil- or soybean oil-fed mice showed an isolation stress-induced increase in the HSP70 mRNA expression level of the spleen (Fig. 3A), indicating that the response of splenic lymphocytes to the isolation stress was greater in the olive oil-fed mice than in the soybean oil- or fish oil-fed mice. Environmental or chemical stress causes the destabilization of protein conformation, leading to protein oxidation, unfolding and aggregation.\textsuperscript{27} It is well established that oxidized, unfolded, and aggregated proteins in mammalian cells are primarily degraded via the 26S proteasome system to prevent adverse consequences to cell maintenance and proliferation.\textsuperscript{28} Therefore, the proteasome activities should be enhanced in response to stress. Following an H\(_2\)O\(_2\) treatment (a model of oxidative stress), the expression levels of mRNA and protein for proteasome subunits were up-regulated in an SH-SYSY rat neural cell line associated with the promotion of protein oxidation.\textsuperscript{29} In the olive oil-fed, but not fish oil-fed mice, the isolation stress increased the expression level of mRNA for splenic proteasome subunits PSMB1, PSMA1 and PSMC3 (Fig. 3C, D and E). It is envisaged that the isolation stress-induced destabilization of protein conformation in splenic lymphocytes may have been more profound in the olive oil-fed mice than in the fish oil-fed mice.

In summary, dietary olive oil caused greater modulation of lymphocyte immunological activities after a 2-week isolation stress exposure than dietary soybean oil or fish oil. This result suggests that excessive dietary OA supplementation and/or moderate ingestion of PUFAs is responsible for the modulation of lymphocyte immune functions under social isolation stress. To clarify the exact mechanism(s) underlying the differences in the degree of modulation resulting from dietary oils with different fatty acid compositions requires further investigation.

References

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