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# SODIUM GLUTAMATE ALTERS LIFESPAN, STRESS RESISTANCE AND METABOLISM IN *DROSOPHILA*

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**Background.** Sodium glutamate (SG) is a widely used flavor enhancer that is regularly consumed by many people worldwide. Despite its widespread use, the safety of SG remains a subject of debate, as existing experimental studies report conflicting results. Additional research is necessary to better understand its biological effects. In this study, we investigated the impact of SG consumption on lifespan, stress resistance, feeding behavior, and metabolism in the fruit fly *Drosophila melanogaster*.

**Materials and Methods.** To assess physiological and biochemical parameters, flies were reared for 15 days on a control diet or food supplemented with SG. Lifespan, resistance to oxidative stress and starvation, and feeding rate were assessed. In addition, we analyzed the levels of key metabolites, including glucose, glycogen, and triacylglycerides, to evaluate the metabolic consequences of SG intake.

**Results and Discussion.** We showed that consumption of food supplemented with a low concentration of SG (0.1%) increased the lifespan of male flies. However, high concentrations of dietary SG decreased the survival of flies of both sexes. Consumption of SG increased resistance to oxidative stress in females, whereas it decreased resistance to starvation. SG leads to higher overall food consumption in flies if the level of dietary SG is low. Consumption of food supplemented with SG affected carbohydrate and lipid metabolism. We observed a decrease in triacylglycerides in flies of both sexes under SG treatment. However, the effects of SG on glucose and glycogen contents were gender-specific.

**Conclusion.** SG influences lifespan in a sex-specific and dose-dependent manner. Excessive intake significantly alters physiological traits in *Drosophila*, including metabolism. Specifically, dietary SG reduced body glycogen levels in males but increased it in females, while triglyceride levels decreased in both sexes under SG treatment, indicating improved lipid utilization. These findings highlight distinct sex-based metabolic responses to SG consumption.

***Keywords:*** monosodium glutamate, metabolism, lifespan, nutrition

## INTRODUCTION

The sodium salt of L-glutamic acid, known as sodium glutamate (SG), is a widely used flavor enhancer (E621) (Bahadoran *et al.*, 2019). SG is produced by the fermentation of starch, sugar beets, sugar cane, or molasses (Gottardo *et al.*, 2022). According to the approval of the US Food and Drug Administration, SG is a safe substance (US Food and Drug Administration, 2012). However, numerous studies have suggested that SG is a harmful component that induces obesity, T2DM, hypertension, and metabolic syndrome (Bahadoran *et al.*, 2019; Insawang *et al.*, 2012).

In water solutions, SG dissolves to 78 % of glutamic acid and 22 % of sodium. Glutamate is the most abundant amino acid of dietary protein and is intensively metabolized in the intestine (Burrin and Stoll, 2009). Moreover, the metabolization of glutamate is crucial to support intermediary metabolism and energy production via the Krebs pathway (Sanchez & Demain, 2008). Glutamate may act as a precursor for the synthesis of reduced glutathione (GSH) (Zhang *et al.*, 2024). While glutamate plays essential physiological roles, some studies have reported that excessive intake of monosodium glutamate may contribute to oxidative stress-related toxicity (Zanfirescu *et al.*, 2019).

Toxicological evaluation of SG was previously conducted using fruit fly *Drosophila melanogaster* (Abolaji *et al.*, 2017; Chourasiya *et al.*, 2021; Kasozi *et al.*, 2018). Studies have shown biological safety of low doses of SG (0.04%, 0.2%, 1%, 5%) in males *Drosophila* $W^{1118}$ strain (Kasozi *et al.*, 2018). Lifespan-shortening effects of long-term exposure to SG were found in flies of both sexes of the short-lived *Harwich* strain, which was associated with oxidative stress induced by SG (Abolaji *et al.*, 2017; Chourasiya *et al.*, 2021).

Although a lot of evidence suggests that SG is an inducer of oxidative stress, the effects of SG on carbohydrate and lipid metabolism, which contributes significantly to lifespan in *Drosophila*, is not completely understood. Hence, there is a need to study the effects of SG on metabolism in flies of both sexes. The study aimed to determine the effects of SG on the level of certain metabolites, including circulating glucose and body glucose, as well as stored glycogen and triglycerides (TAG). Moreover, we also plan to investigate some physiological effects of SG on flies of both sexes of wild-type *Drosophila* (*Canton-S*). Studying the effect of SG on *Drosophila* as a model organism will shed light on various aspects of SG biological activities.

## MATERIALS AND METHODS

**Fly husbandry.** Fruit flies *Drosophila melanogaster* of the *Canton-S* line were obtained from Bloomington Stock Center (Bloomington, IN, United States). The flies were cultured in a standard medium (5% sucrose, 5% yeast, 6% cornmeal, 1% agar,

0.18% methyl 4-hydroxyparabenzoic acid (methylparaben), and 0.6% propionic acid) at a density of 70–100 eggs per vial, 25°C, 60% humidity, and 12:12 h photoperiod. Immediately after eclosion, flies were transferred to a fresh medium and held for four days until the beginning of the experiments.

**Experimental design.** Four-day-old flies were separated by sex under light $CO_2$ anesthesia and transferred into demographic cages. To assess physiological and biochemical parameters, flies were reared for 15 days on a control diet or food supplemented with sodium glutamate (SG). The control diet contained 5% sucrose, 5% yeast, 1.2% agar, and 0.18% methylparaben. SG was added to the medium at concentrations of 0.1%, 0.5%, and 5%. Dosing concentrations of SG were chosen based on prior studies and regulatory guidelines. The lower doses approximate typical dietary exposure (Insawang *et al.*, 2012), while 5% serves as a high-dose level to assess potential toxic effects. SG was mixed with freshly prepared medium cooled to 70 °C. Every two days, the experimental media were replaced with fresh ones. After 15 days, the experimental flies were used to determine feeding rate, stress resistance, mobility, or frozen for subsequent measurements.

**Lifespan assay.** About 150 flies of each sex were transferred into 1.5 L demographic cages with a plastic vial filled with 5 mL of control or experimental food and attached to the side of the cage. Food was changed every second day, and dead flies were removed and recorded. The experiment was run in two biological replicates.

**Feeding assay.** Twenty flies that had been kept on experimental media in groups for fifteen days were allowed to feed for 75 min during the daytime on an experimental medium supplemented with 0.5% erioglaucine. After 75 min of feeding, flies were frozen in liquid nitrogen for further analysis. Next, flies were each homogenized in 50 mM phosphate buffer (pH 7.5). Homogenates were centrifuged twice (16000g, 10 min, 25 °C) and aliquots of the final supernatants were used to measure absorbance. Optical density was determined at a wavelength of 629 nm on a Spekol 211 spectrophotometer (Carl Zeiss, Jena, Germany). The amount of consumed food was expressed as nanograms of food ingested per fly over 75 min (ng/fly/75 min). The amount of medium consumed was used to calculate the amount of SG consumed.

**Mobility test.** Ten flies of each cohort were transferred to clean, empty vials with cotton stoppers. Flies were gently tapped to the bottom of the vial and given 20 s to climb 5 cm. The number of flies that passed a distance of 5 cm was counted. Each vial was tested three times and means were calculated. The experiment was run in four independent biological replicates.

**Resistance to starvation and oxidative stress.** To determine the resistance to starvation, 10–15 flies reared on control and experimental media were placed in 20 mL plastic tubes with 3 mL of 0.5% agarose gel containing 0.18% of added methylparaben. To test for oxidative stress resistance, 20 mM menadione in 5% sucrose was used. Menadione is a redox-cycling agent that generates intracellular reactive oxygen species (ROS) such as superoxide anion radicals. The number of dead flies was recorded every day at 9 AM, 3 PM, and 9 PM until the death of the last fly in each group. The experiments were performed in two biological replicates.

**Metabolite levels.** To measure the levels of glucose and glycogen in hemolymph and the body, flies were decapitated and centrifuged to extract hemolymph (3000g, 5 min). Pre-weighted bodies were homogenized in 50 mM sodium buffer, centrifuged, and used for the determination of glucose and glycogen levels. Measurements were

performed using a glucose assay kit Glucose-Mono-400-P (Reagent PJSC), according to the manufacturer's instructions. Glycogen was converted into glucose by amyloglucosidase from *Aspergillus niger* (25 °C, 4 h). For TAG determination, flies were weighed, homogenized in 200 mM PBST (phosphate buffered saline containing 0.05% Triton X100) boiled, and centrifuged (13000g, 10 min). The resulting supernatants were used for TAG assay with Triacylglycerol-Mono-100 mono-reagent (Reagent PJSC). Females of all genotypes were tested in four independent replicates.

**Statistical analysis.** Statistical processing of the data was performed using GraphPad Prism 8 software. The Log-rank test was used to analyze survival curves. The Dunnett test was used to determine a significant difference between groups. Data are shown as mean ± SEM; $p$ value < 0.05 was considered significant.

## RESULTS AND DISCUSSION

There are a lot of controversial studies about the safety of using SG because of some misunderstandings concerning the doses of SG and the appropriate model objects. Moreover, there are very few studies that used *Drosophila* as a model to test SG biological effects (Abolaji *et al.*, 2017; Chourasiya *et al.*, 2021; Kasozi *et al.*, 2018). In the current study, *Drosophila* male and female flies were fed media with SG at a range of concentrations, in order to analyze fly sensitivity to SG and its effects on carbohydrate and lipid metabolism. We showed that dietary SG significantly affected *Drosophila* lifespan (**Fig. 1*A*,*B***). Interestingly, consumption of the medium with 0.1% SG led to lifespan extension in males (**Fig. 1*B***; $p$ = 0.02). An increase in median lifespan by 6 % was found (**Fig. 1*D***; $p$ = 0.03). However, diet supplementation with 0.5 and 5% of SG caused shortening of male lifespan (**Fig. 1*A***; $p$ < 0.03). Similarly, consumption of food supplemented with SG at concentrations of 0.5% and 5% shortened the lifespan of female flies (**Fig. 1*B***; $p$ <0.0001). The median lifespan of control male and female flies was approximately 58 and 68 days, respectively (**Fig. 1*C*,*D***). We observed significantly lower median lifespan in flies of both genders, which were exposed to 0.5% and 5% of SG (**Fig. 1*C*,*D***; $p$ <0.03). A decreased lifespan at high SG concentrations may be associated with increased reactive oxygen and nitrogen species, as well as $H_2O_2$ generations in flies exposed to SG, as was reported in a previous study (Abolaji *et al.*, 2017). However, this assumption remains to be confirmed through additional experimental evidence. Previous studies showed no significant influence of SG at a range of concentrations 0.04%–5% on negative geotaxis and lifespan in $W^{1118}$ male *Drosophila* (Kasozi *et al.*, 2018). Another study demonstrated a reduction in the lifespan of *Drosophila* under SG treatment at concentrations 0.1, 0.5, and 2.5 g/kg diet that corresponds to 0.01%, 0.05%, and 0.25% (Abolaji *et al.*, 2017). An extended lifespan under low SG doses suggests that SG may cause a hormetic-like trend, increasing survival at low concentrations while decreasing survival at high doses.

Lifespan-extending effects of some interventions are often associated with increased resistance of an organism to multiple stresses (Soo *et al.*, 2023). Dietary SG affects the resistance of *D. melanogaster* to starvation and menadione-induced oxidative stress. Consumption of food with 5% of SG significantly reduced resistance to starvation in female flies as compared to flies of the control group (**Fig. 2*B***; $p$ <0.0001). Starvation resistance of males was not affected by SG exposure (**Fig. 2*A***). The observed decrease in TAG levels in SG-treated flies may underlie their reduced capacity to withstand starvation, highlighting a possible link between altered lipid storage and stress susceptibility.

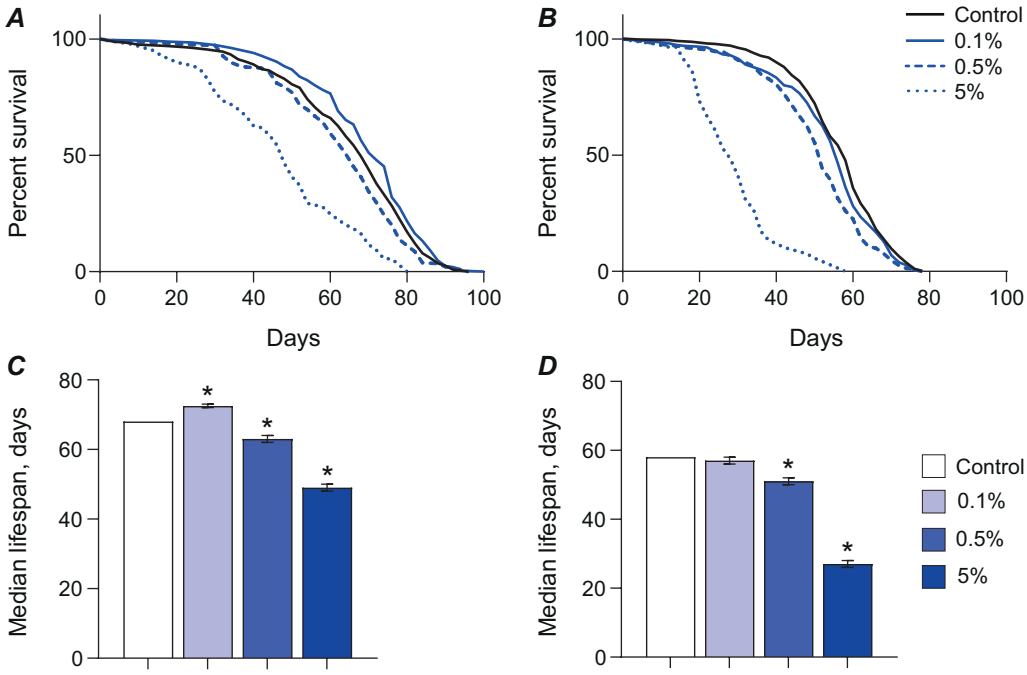


**Fig. 1.** Survival curves (***A*** – males; ***B*** – females) and median lifespan (***C*** – males; ***D*** – females) of flies exposed to SG. In A and B each curve represents the percentage of alive flies within respect time. The cohorts were compared using a Log-rank test. In C–F results represent the mean ± SEM of 2 bilogical replicates per group. Group comparisons were performed using Dunnett's test. The asterisk indicates a significant difference between groups with $p$ <0.05

Consumption of the medium with SG at a concentration of 0.1% caused a lower resistance to oxidative stress induced by menadione in males as compared to the control group (**Fig. 2*C***; $p$ <0.0001). However, females who were exposed to SG at concentrations of 0.5% and 5% had a higher resistance toward 20 mM menadione as compared to the control (**Fig. 2*D***; $p$ <0.03). A higher oxidative stress resistance in females may be associated with an induced adaptive response to short-term exposure to SG via induction of antioxidant enzyme activities and total thiol level (Abolaji *et al.*, 2017).

Consumption of SG is often associated with neuronal damage and impaired motor activity (Poon & Cameron, 1978; Xiong *et al.*, 2009). SG supplementation impaired a negative geotaxis response only in female flies (**Fig. 3*F***). Females that consumed a diet with 5% SG showed approximately 11 % lower performance as compared to the control group ($p$ = 0.04). A decreased motor activity in female flies exposed to SG at a concentration of 5% can be associated with neurotoxic effects of high doses of SG, which was previously seen in animal studies (Liang *et al.*, 2024). While neurotoxicity has been documented in mammalian studies (Liang et al., 2024), this remains a hypothesis in the context of *Drosophila*. Interestingly, there were no effects of SG on locomotion in males (**Fig. 3*E***).

As a flavor enhancer, SG leads to a higher overall food consumption in flies of both sexes if the level of dietary SG is low. The control male consumed 24 nL of medium per 75 minutes. A higher volume of medium – 1.7-fold as compared to the control – was consumed by the male flies exposed to 0.1% of SG (**Fig. 3*A***; $p$ = 0.001). The control

female consumed 62 nL of the medium per 75 min. Similarly, females exposed to 0.1% of SG consumed 29 % higher amounts of food as compared to the control (**Fig. 3*B***; $p$ = 0.04). Higher concentrations of SG in the medium led to proportionally greater amounts of it being consumed by the flies of both sexes as compared to appropriate controls (**Fig. 3*C*,*D***; $p$ <0.05). Our study is in good agreement with previous studies that have demonstrated stimulating appetite during ingestion and enhancing post-ingestive satiety effects (Masic & Yeomans, 2014). SG enhances the hypothalamic center for appetite (Kayode *et al.*, 2023). Our result aligns with previous studies suggesting that the optimal concentration of SG for enhancing the flavor of foods is between 0.1% and 0.8% by weight (Beyreuther *et al.*, 2007). Similar to humans, fruit flies can detect SG, experiencing the umami taste (Croset *et al.*, 2016). Z. Yang *et al.*, (2018) show that in *D. melanogaster*, L-glutamate, together with L-alanine and L-aspartate, promotes food consumption. These amino acids activate six neurons in the brain which serve as amino acid sensors. This activation facilitates the identification, evaluation, and consumption of protein-rich food sources (Yang *et al.*, 2018).

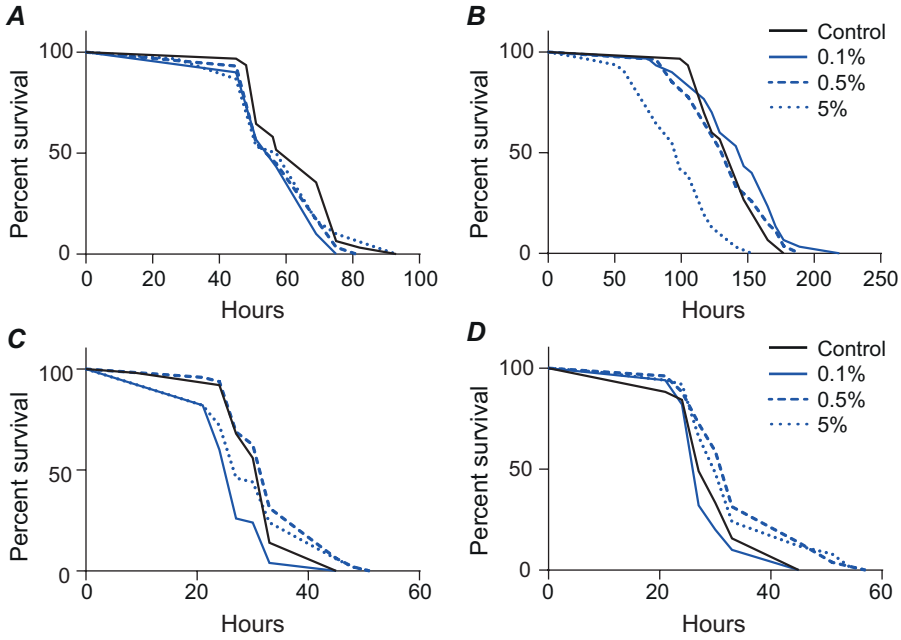


**Fig. 2.** Resistance to starvation (***A*** – males, ***B*** – females) and resistance to menadione treatment (***C*** – males, ***D*** – females) in flies fed for 15 days by diets supplemented with SG. Each curve represents the percentage of alive flies within respect time. The cohorts were compared using a Log-rank test

Food consumption has a direct effect on metabolic processes within an organism. Lipids and carbohydrates represent a primary fraction of the body's energy pool and shifts in their homeostasis have a significant impact on lifespan. Consumption of food with 0.1% of SG decreased the amount of body glucose in females by 21 % (**Fig. 4*B***; $p$ = 0.01), with no impact on males (**Fig. 4*A***). Males reared on food with 0.5% of SG showed a 41 % increase in the levels of circulating glucose, whereas females reared on food with 5% of SG showed a 28 % decrease in the levels of circulating glucose as compared to the control (**Fig. 4*C*,*D***; $p$ < 0.05).

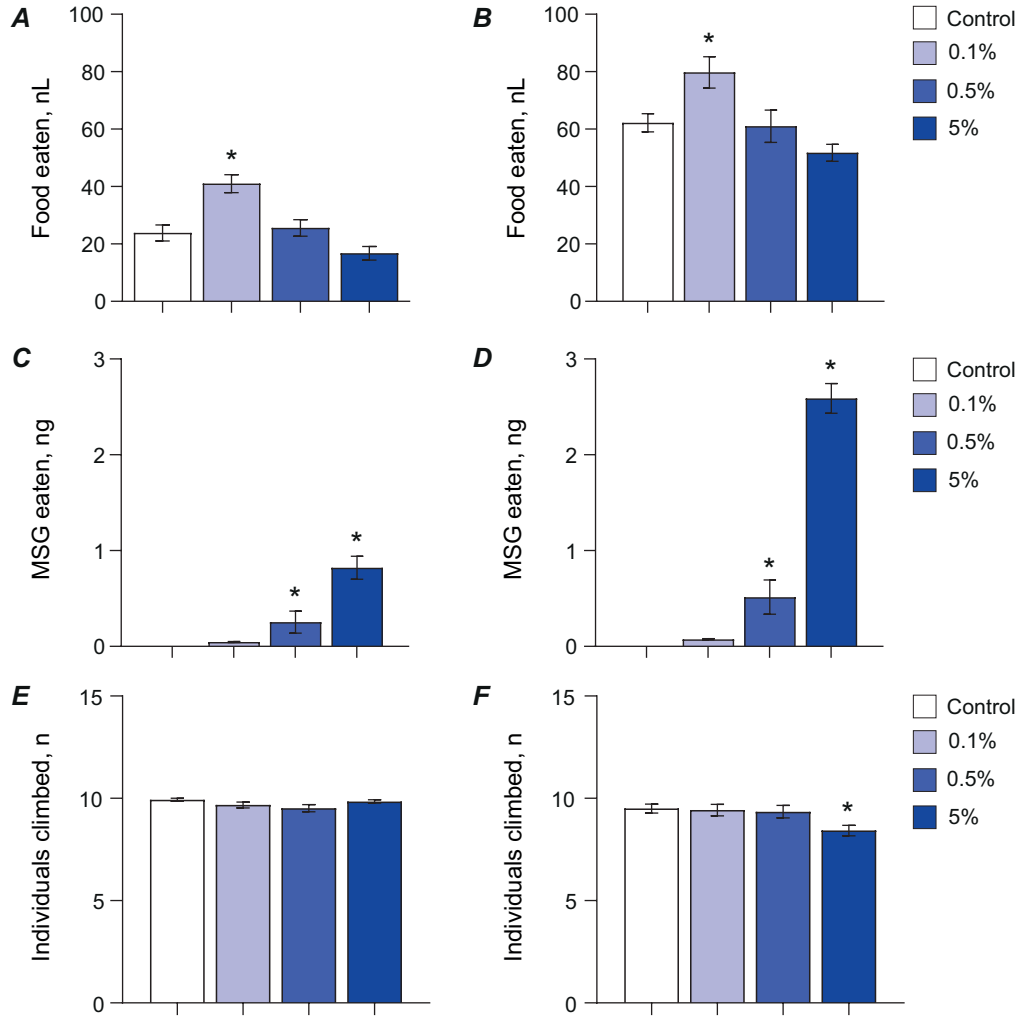


**Fig. 3.** The effects of dietary SG on the appetite of male (***A***) and female (***B***) flies and climbing ability (***E*** – males; ***F*** – females). The amount of SG eaten by males (***C***) and females (***D***) *Drosophila*. Data are mean ± SEM, n = 4–6 (biological replicates). Group comparisons were performed using Dunnett's test. The asterisk indicates a significant difference between groups

Glycogen and triglycerides (TAG) are the most important sources of calories required to maintain energy homeostasis in animals, including *D. melanogaster*. Glycogen levels in males who consumed food with SG in the concentration of 5% were lower by 35 % (**Fig. 5*A***; $p = 0.04$). However, we observed a 30% higher glycogen pool in females fed by medium with 0.5% of SG as compared to the control (**Fig. 5*B***; $p = 0.001$). TAG levels were 44 % lower in males (at 0.1% SG supplementation) and by ~25 % in females fed diets with 0.1–5% of SG (**Fig. 5*C*,*D***; $p < 0.02$). We also observed a higher susceptibility to starvation in female flies that may be caused by a decreased TAG pool observed in the current study under SG exposure. The deposition of storage fat in the form of TAG is an evolutionarily conserved strategy to cope with metabolic stress.

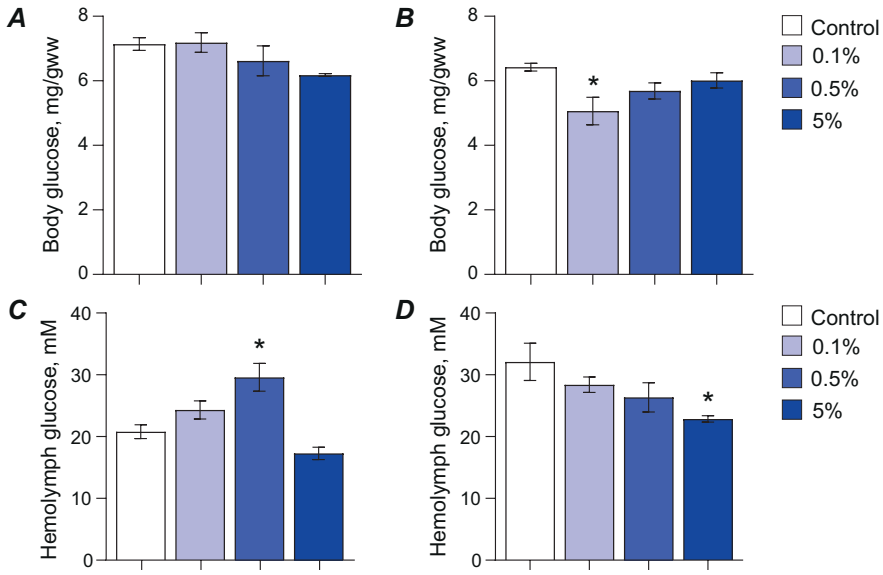


**Fig. 4.** Levels of body glucose (***A*** – males; ***B*** – females) and hemolymph glucose (***C*** – males; ***D*** – females) in adult *Drosophila* that were fed by either control food or food supplemented with SG at concentrations: 0.1%, 0.5%, and 5%. Results represent the mean ± SEM of 4–6 biological replicates per group. Group comparisons were performed using Dunnett's test. The asterisk indicates a significant difference between groups with $p < 0.05$

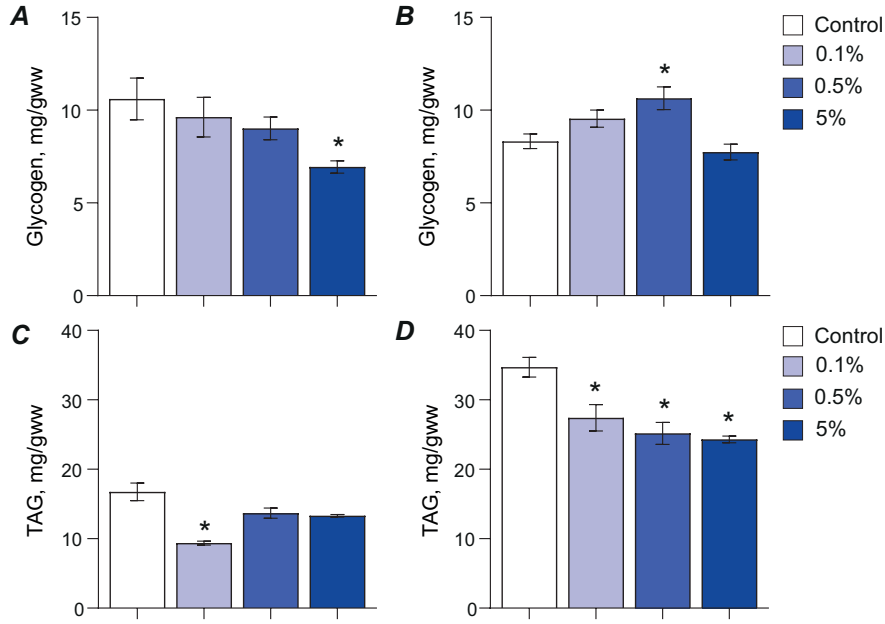


**Fig. 5.** Levels of stored metabolites: glycogen (***A*** – males; ***B*** – females) and TAG (***C*** – males; ***D*** – females) in adult *Drosophila* that were fed by either control food or food supplemented with SG at concentrations: 0.1%, 0.5%, and 5%. Results represent the mean ± SEM of 4-6 biological replicates per group. Group comparisons were performed using Dunnett's test. The asterisk indicates a significant difference between groups with $p < 0.05$

Interestingly, we found some gender-specific effects of SG on the levels of glucose and glycogen in *Drosophila*. Indeed, in males exposed to SG, the level of circulating glucose was higher, while the glycogen pool was significantly depleted. We found controversial effects of SG in females; decreased body and hemolymph glucose were accompanied by higher glycogen storage. Being consumed, SG dissolves into sodium ions and glutamate, which is readily absorbed in the gut and enters into the Krebs cycle to produce energy (Burrin & Stoll, 2009). The induction of energy production by glutamate would be associated with an increased glucose breakdown (Mlawer *et al.*, 2024). In our study, we investigated SG effects on metabolite levels in *Drosophila* for the first time. However, some controversial studies tested glucose levels in mice exposed to SG. One study showed that administration of 2 mg/g SG resulted in a decrease in blood glucose concentration in male mice (Ahluwalia & Malik, 1989), but another demonstrated elevated plasma glucose and insulin in SG-treated mice (Cameron *et al.*, 1976).

Gender differences in our investigated parameters may be caused by distinctions in organs, systems, and signaling networks in males and females *Drosophila* (Lushchak *et al.*, 2023). Our current study confirmed previous observations that males and females of *Drosophila* have different sensitivities to nutritional interventions (Lushchak *et al.*, 2023). We found that female flies are more susceptible to SG due to a higher amount of food and SG consumed. Females are characterized by a larger gut than males (Millington *et al.*, 2020) which results in a higher volume of medium eaten and, in turn, a higher amount of SG intake observed in our study.

## CONCLUSION

In summary, we hypothesize that low doses of SG are safe. Moreover, low-dose sodium glutamate supplementation (0.1%) was associated with a modest but significant increase in male lifespan, suggesting potential beneficial effects at limited exposure levels. In contrast, higher concentrations produced adverse physiological and metabolic outcomes in a sex-specific manner. Future studies should include direct assessment of oxidative stress markers (e.g., ROS levels), mitochondrial function assays, and transcriptomic analysis of key metabolic and stress-response genes to clarify the mechanisms driving the observed physiological changes.

## COMPLIANCE WITH ETHICAL STANDARDS

**Conflict of Interest**: the authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

**Human Rights.** this article does not contain any studies with human subjects performed by any of the authors.

## AUTHOR CONTRIBUTIONS

Conceptualization, [O.L.]; methodology, [O.L.]; validation, [O.L.]; formal analysis, [O.L.; O.S.]; investigation, [V.P.]; resources, [O.L.]; data curation, [O.L.]; writing – original draft preparation, [V.P.; O.S.]; writing – review and editing, [O.S.; O.L.]; visualization, [O.S.] supervision, [O.L.]; project administration, [O.L.]; funding acquisition, [O.L.].

All authors have read and agreed to the published version of the manuscript.

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# ГЛУТАМАТ НАТРІЮ ВПЛИВАЄ НА ТРИВАЛІСТЬ ЖИТТЯ, СТІЙКІСТЬ ДО СТРЕСУ ТА МЕТАБОЛІЗМ *DROSOPHILA*

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**Обґрунтування.** Глутамат натрію (ГН) широко використовують як підсилювач смаку, і його регулярно вживають багато людей у всьому світі. Незважаючи на широке використання, безпечність ГН залишається предметом дискусій, оскільки попередні експериментальні дослідження дають суперечливі результати. Для кращого розуміння його біологічних ефектів необхідні додаткові дослідження. У цій роботі ми вивчали вплив споживання ГН на тривалість життя, стресостійкість, харчову поведінку і метаболізм плодових мушок *Drosophila melanogaster*.

**Матеріали та методи.** Для оцінки фізіологічних і біохімічних показників мух вирощували протягом 15 днів на стандартному раціоні або на кормі з додаванням ГН. Оцінювали тривалість життя, стійкість до оксидативного стресу, голодування й інтенсивність споживання корму. Крім того, ми проаналізували рівні ключових метаболітів (глюкози, глікогену і триацилгліцеридів), щоб оцінити метаболічні наслідки споживання ГН.

**Результати.** З'ясовано, що споживання корму з низькою концентрацією ГН (0,1%) продовжувало тривалість життя самців мух. Однак високі концентрації ГН у харчовому раціоні мух знижували виживання мух обох статей. Споживання ГН призводило до підвищення стійкості до окислювального стресу у самок, тоді як знижувало стійкість до голодування. Глутамат натрію зумовлює збільшення загального споживання корму мухами, якщо рівень ГН у раціоні низький. Споживання корму з додаванням ГН впливало на вуглеводний і ліпідний обмін. Спостерігали зниження рівня триацилгліцеридів у мух обох статей за дії ГН. Однак вплив ГН на вміст глюкози та глікогену залежав від статі.

**Висновки.** Глутамат натрію впливає на тривалість життя залежно від статі й дози. Надмірне споживання значно впливає на фізіологічні показники дрозофіли, в тому числі й на метаболізм. Зокрема, ГН знижує рівень глікогену в тілі самців, але підвищує його у самок, тоді як рівень тригліцеридів є нижчим у обох статей за споживання корму із ГН, що свідчить про покращення утилізації ліпідів. Ці дані свідчать про різні метаболічні реакції на споживання ГН, що залежать від статі.

***Ключові слова:*** глутамат натрію, метаболізм, тривалість життя, харчування

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