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ORIGINAL ARTICLE

The role of glutamatergic and GABAergic systems on serotonin- induced feeding behavior in chicken

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Abstract It has been reported that serotonin can modulate glutamate and GABA release in central nervous system (CNS). The present study was designed to examine the role of glutamatergic and GABAergic systems on serotonin- induced feeding behavior in chickens. In Experiment 1 intracerebroventricular (ICV) injection of MK- 801(NMDA receptor antagonist, 15 nmol) performed followed by serotonin (10 μg). In experiments 2, 3, 4, 5, 6 and 7 prior to serotonin injection, chickens received CNQX (AMPA/kainate receptor antagonist, 390 nmol), AIDA (mGluR1 antagonist, 2 nmol), LY341495 (mGluR2 antagonist, 150 nmol), UBP1112 (mGluR3 antagonist, 2 nmol), picrotoxin (GABA A receptor antagonist, 0.5 μg), CGP54626 (GABAB receptor antagonist, 20 ng) respectively. Cumulative food intake was determined at 3 h post injection. The results of this study showed that the hypophagic effect of serotonin was significantly attenuated by pretreatment with MK- 801 and CNQX ($p<0.05$) but AIDA, LY341495 and UBP1112 had no effect ($p>0.05$). Also, the inhibitory effect of serotonin on food intake was amplified by picrotoxin ($p<0.05$) while CGP54626 had no effect ($p>0.05$). These results suggest that serotonin as a modulator probably interacts with glutamatergic (via NMDA and AMPA/Kainate receptors) and GABAergic (via GABAA receptor) systems on feeding behavior in chicken.

Keywords Serotonin · Glutamate · GABA · Food intake · Chicken

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Introduction

Nowadays numerous neurotransmitters involved in regulation of food intake have been identified; among them are serotonin (5-HT), glutamate and GABA. The neurotransmitter 5-HT seems have important role in the central control of feeding behavior not only in mammals but also in avian species. It has been observed that in Leghorn chickens deprived of food for 24 h (FD24) injections of 5-HT intracerebroventricularly (ICV) causes a significant decrease in food intake (Zendehdel et al. 2012a, b). Another neurotransmitter known to be involved in feeding behavior in avian species is glutamate. It has been reported that glutamate, the most abundant excitatory amino acid in the central nervous system (CNS), attenuates food intake in broiler cockerels and this effect is probably mediated by both ionotropic and metabotropic receptors (Zeni et al. 2000; Baghbanzadeh and Babapour 2007; Zendehdel et al. 2009). In addition, microinjections of NMDA and AMPA-kainite receptor antagonists into ventral striatal and ventral pallidal areas of the pigeon induced feeding behavior (Da Silva et al. 2003). By contrast, the results of another study showed that the ICV injection of DL-AP5 (NMDA receptor antagonist) dose dependently increased food consumption in FD3 broiler cockerels (Taati et al. 2011). However, researchers have shown that stimulation of lateral hypothalamic AMPA receptors (glutamate ionotropic receptors) induced feeding in rats (Hettes et al. 2010). In contrast with the role of 5-HT and glutamate in decrease of food intake in birds, GABA, the principal inhibitory neurotransmitter in the CNS, appears mostly to increase food intake in avian species (Jonaidi et al. 2012). Findings have suggested that the ICV injection of muscimol, a $GABA_A$ agonist, in layer type chicks (Bungo et al. 2003) and broilers (Jonaidi et al. 2002; Tajalli et al. 2006; Zendehdel et al. 2008, 2009) and baclofen, a $GABA_B$ agonist, in layer strain chicks (Bungo et al. 2003) increased food consumption while baclofen had no

effect on food intake in broilers (Jonaidi et al. 2002; Bungo et al. 2003). Also, picrotoxin, a $GABA_A$ receptor antagonist, decreased food intake in chicks indicating a stimulatory effect of $GABA_A$ receptors on food intake (Jonaidi et al. 2012).

Numerous studies have reported that 5-HT can modulate excitatory and inhibitory effects respectively mediated by glutamate and GABA (Ciranna 2006; Dawson et al. 2001; Mlinar et al. 2003; Katsurabayashi et al. 2003; Koyama et al. 2002). Modulatory effect of 5-HT on glutamate-mediated stimulatory transmission has been described in several CNS regions, especially in those controlling cognition and nociception (Ciranna 2006). Modulation of GABA-mediated inhibitory transmission by 5-HT, in parallel with glutamate interactions, has been noticed in structures involved in learning and memory, sensory processing and nociception (Ciranna 2006).

On the basis of these findings and considering the participation of 5-HT, glutamate and GABA on feeding behavior in birds and the known role of 5-HT as a modulator of glutamate and GABA transmissions in some brain regions, we hypothesized that 5-HT ergic system possibly modulates glutamatergic and GABAergic systems involved in food intake of birds. Therefore, the hypothesis of present study was to investigate whether blocking glutamate and GABA receptors can influence 5-HT -induced feeding response in 3 h food-deprived chickens.

Materials and methods

Animals

One hundred and ninety-two day-old Ross (308) cockerels (Eshragh Co, Iran) were reared in heated batteries with continuous lighting until 3 weeks of age. Before the experiments, birds were weighed and randomly assigned into experimental groups (average live body weight (LBW) 950±30 gr in each group). The chickens had free access to a mash diet (21 % protein and 2,869 kcal/kg of metabolizable energy; Pars animal Feed, Iran) and water. At approximately 2 weeks of age, the birds were transferred to individual cages. The room was maintained at a temperature of 22±1 °C with 50 % humidity, and continuously lighted (Olanrewaju et al. 2006). Animal handling and experimental procedures were performed according to the Guide for the Care and Use of Laboratory Animals by the National Institutes of Health (USA) and the current laws of the Iranian government.

Drugs

5-HT, MK- 801 (NMDA receptor antagonist), CNQX (AMPA/kainate receptor antagonist), AIDA (mGluR1 antagonist), LY341495 (mGluR2 antagonist), UBP1112 (mGluR3 antagonist), picrotoxin ($GABA_A$ receptor antagonist), CGP54626 ($GABA_B$ receptor antagonist), were purchased from Tocris Co (UK). All solutions were prepared in a 0.9 % pyrogen-free NaCl solution (saline) that served as the vehicle control.

Surgical preparation

At 3 weeks of age, the broilers were anesthetized with xylazin [1 mg/kg^{-1}, intramuscular (IM) injection] and ketamine (30 mg/kg^{-1}, IM) (Thurmon et al. 1996). A 23-gauge thin-walled stainless steel guide cannula (Razipakhsh, Iran) was then stereotaxically implanted into the right lateral ventricle, according to the technique described previously (Denbow et al. 1981). The stereotaxic specifications were anterior/posterior: 6.7 mm, lateral: 0.7 mm and horizontal: 3.5~4 mm below the dura mater with the head oriented as described previously (Van Tienhoven and Juhaz 1962). The cannula was secured with three stainless steel screws placed into the calvaria surrounding each guide cannula. Acrylic dental cement (Pars Acryl, Iran) was then applied to the screws and guide cannula. An orthodontic No. 014 wire (American Orthodontics, USA) trimmed to the exact length of the guide cannula was inserted into the guide cannula when the chickens were not being used for the experiments. Lincospectin (Razak, Iran) was applied to the incision to prevent possible infections. The chickens were allowed a minimum of 5 days to recover prior to receiving injections of solutions.

Experimental procedures

To determine the possible role of central glutamate and GABA receptors on 5-HT induced feeding behavior, the effects of centrally administered glutamate and GABA receptor antagonists on 5-HT -induced eating responses of the chickens were investigated. Injections were conducted with a 29-gauge, thin-walled stainless steel injecting cannula (Razipakhsh, Iran) that extended 1.0 mm beyond the guide cannula. This injecting cannula was connected through 60-cm polyethylene-20 tubing (Parsian tube, Iran) to a 10 μl Hamilton syringe (Hamilton, Switzerland). All drugs were injected over a period of 60 s. The solution was then allowed to diffuse from the tip of the cannula into the ventricle for an additional 60 s. All experimental procedures were performed from 10:00 am to 4:00 pm. The chickens were removed from the cages, restrained by hand, and then returned to the cages after receiving the injection. The birds were handled and mock injected daily during the 5-day recovery period in order to adapt them to the injection procedure. Three hours before initiating the experiments, the animals were deprived of food (FD3). Each individual bird received two injections with 15 min interval. Immediately after the second injection chickens were returned

Table 1 Treatment procedure in experiment 1

First injection	Second injection	Treatments
Saline	Saline	Saline+Saline[a] (n=6)
Saline	Serotonin (10 μg)	Saline+Serotonin (n=6)
MK- 801 (15 nmol)	Saline	MK- 801+saline (n=6)
MK- 801 (15 nmol)	Serotonin (10 μg)	MK-801+Serotonin (n=6)

[a] *S* 0.9 % NaCl: control

to their individual cages, fresh food was supplied and cumulative food intake (gr) was measured at 30, 60, 120 and 180 min post second injection. Tubing and syringes were kept in 70 % ethanol, and the glassware was autoclaved to render all materials pyrogen-free. In this study, all control groups like treatment groups received two injections, 5 μl saline, with 15 min interval.

Experiment 1 was designed to examine the effect of ICV injections of MK- 801 (NMDA receptor antagonist) on 5-HT-induced food intake of FD3 chickens (n=6 per group). Each chicken received two injections. The first injection contained either 0 or 15 nmol MK- 801 in 5 μl of saline. The second injection consisted of either 0 or 10 μg 5-HT in 5 μl saline as described in Table 1 (n=6 per group). All injections for the control group contained only 5 μl of saline. Experiments 2, 3, 4, 5, 6 and 7 were conducted in a manner similar to Experiment 1 except that the chickens received 0 or 390 nmol CNQX (AMPA/kainate receptor antagonist), 0 or 2 nmol AIDA (mGluR1 antagonist), 0 or 150 nmol LY341495 (mGluR2 antagonist), 0 or 2 nmol UBP1112 (mGluR3 antagonist), 0 or 0.5 μg picrotoxin ($GABA_A$ receptor antagonist), 0 or 20 ng CGP54626 ($GABA_B$ receptor antagonist), instead of MK- 801, respectively. Each bird was only used in one experiment. Animals were killed painlessly following the study according the mentioned guidelines. Placement of the guide cannula into the ventricle was verified by the presence of cerebrospinal fluid and ICV injection of methylene blue followed by slicing the frozen brain tissue at the end of each experiment. All animals in experiments 1–7 were deprived of food for 3 h prior to initiating the study. All doses of drugs were calculated based on previous and pilot studies (Zeni et al. 2000; Baghbanzadeh and Babapour 2007; Zendehdel et al. 2009, 2012a, b; Jonaidi and Noori 2012).

Statistical analysis

Cumulative food intake was analyzed by two way analysis of variance (ANOVA) and is presented as the mean ± SEM. For treatments found to have an effect according to the ANOVA using SPSS 16.0 for Windows (SPSS, Inc., Chicago, IL, USA), mean values were compared with post hoc Bonferroni. P-values <0.05 were considered to indicate significant differences between the treatments.

Results

The food intake response to ICV injection of MK- 801, CNQX, AIDA, LY341495, UBP1112, picrotoxin and CGP54626 followed by 5-HT in chickens is presented in Figs. 1, 2, 3, 4, 5, 6, and 7. For the subsequent experiments, a 10-μg dose of serotonin was used because it was found to significantly decrease food consumption in the FD3 birds without affecting other non-ingestive behavioural parameters.

In experiment 1, the inhibitory effect of 5-HT on food intake was decreased by 15 nmol MK- 801 pretreatment ($F_{3,\ 25}$= 34.07) (P<0.05), but 15 nmol MK- 801 alone could not

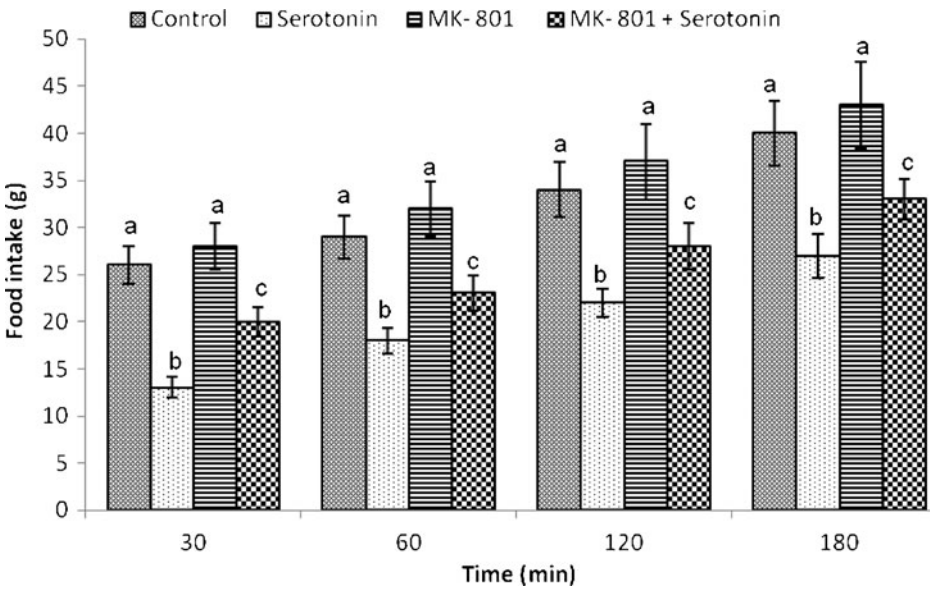

Fig. 1 Effect of ICV injection of MK- 801 (15 nmol) followed by serotonin (10 μg) on food intake in 3-h food deprived chickens. Data are presented as mean ± SEM. Different letters (*a*, *b* and *c*) indicate significant differences between treatments (P<0.05)

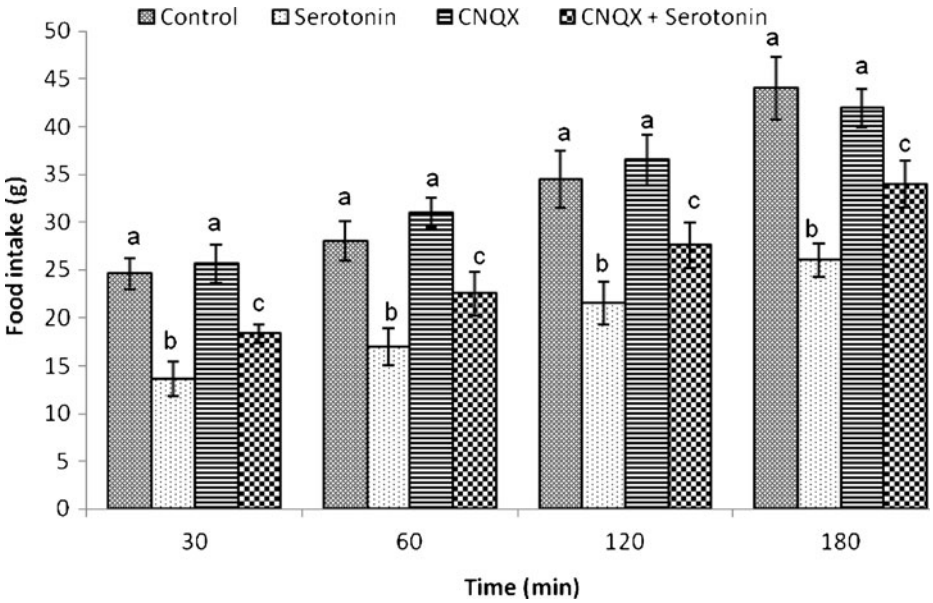

Fig. 2 Effect of ICV injection of CNQX (390 nmol) followed by serotonin (10 μg) on food intake in 3-h food deprived chickens. Data are presented as mean ± SEM. Different letters (*a*, *b* and *c*) indicate significant differences between treatments ($P<0.05$)

alter food intake in FD3 chickens compared to control group ($F_{3,\ 25}=0.08$) ($P>0.05$) (Fig. 1).

In experiment 2, hypophagic effect of 5-HT was significantly attenuated by administration of 390 nmol CNQX in FD3 chickens ($F_{3,\ 25}=23.19$) ($P<0.05$), while 390 nmol CNQX alone had no effect on food intake compared to control group ($F_{3,\ 25}=3.11$) ($P>0.05$) (Fig. 2).

In experiment 3, pretreatment with 2 nmol AIDA had no effect on the hypophagia induced by 5-HT in FD3 chickens ($F_{3,\ 25}=1.43$) ($P>0.05$) (Fig. 3). Furthermore, 2 nmol AIDA alone had no effect on food intake ($F_{3,\ 25}=0.48$) ($P>0.05$) (Fig. 3).

In experiment 4, 150 nmol LY341495 pretreatment did not modify the inhibitory effect of 5-HT on food intake in FD3 chickens ($F_{3,\ 25}=2.46$) ($P>0.05$) (Fig. 4). Also, 150 nmol LY341495 alone had no effect on food intake ($F_{3,\ 25}=1.08$) ($P>0.05$) (Fig. 4).

In experiment 5, pretreatment with 2 nmol UBP1112 had no effect on the hypophagia induced by 5-HT on food intake in FD3 chickens ($F_{3,\ 25}=4.93$) ($P>0.05$) (Fig. 5). Furthermore, 2 nmol UBP1112 alone was not able alter food intake compared to control group ($F_{3,\ 25}=3.85$) ($P>0.05$) (Fig. 5).

In experiment 6, the inhibitory effect of 5-HT on food intake was amplified by 0.5 μg picrotoxin pretreatment in FD3 chickens ($F_{3,\ 25}=18.43$) ($P<0.05$) (Fig. 6). Moreover, picrotoxin (0.5 μg) alone had no significant effect on food intake in chickens compared to control group ($F_{3,\ 25}=2.64$) ($P>0.05$) (Fig. 6).

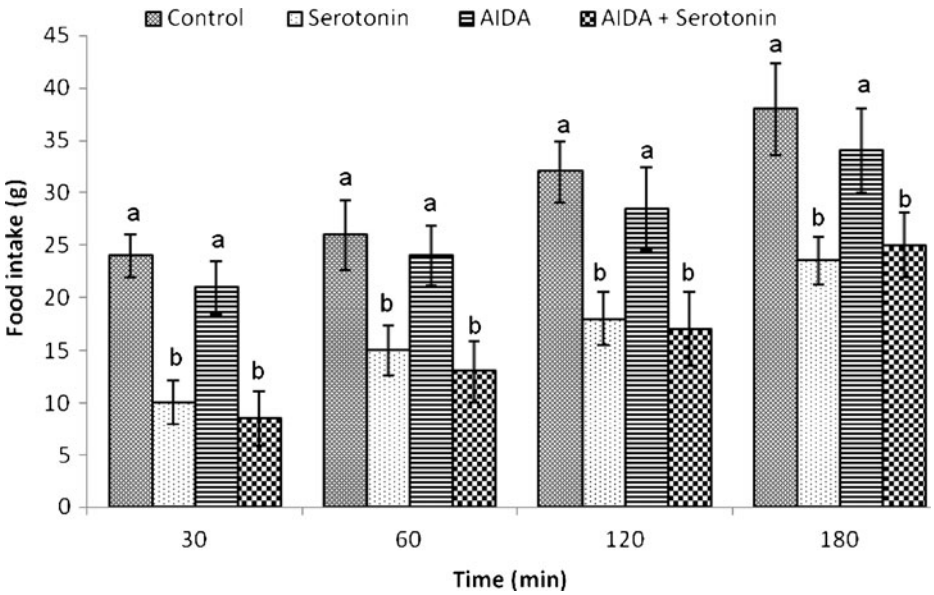

Fig. 3 Effect of ICV injection of AIDA (2 nmol) followed by serotonin (10 μg) on food intake in 3-h food deprived chickens. Data are presented as mean ± SEM. Different letters (*a*, *b*) indicate significant differences between treatments ($P<0.05$)

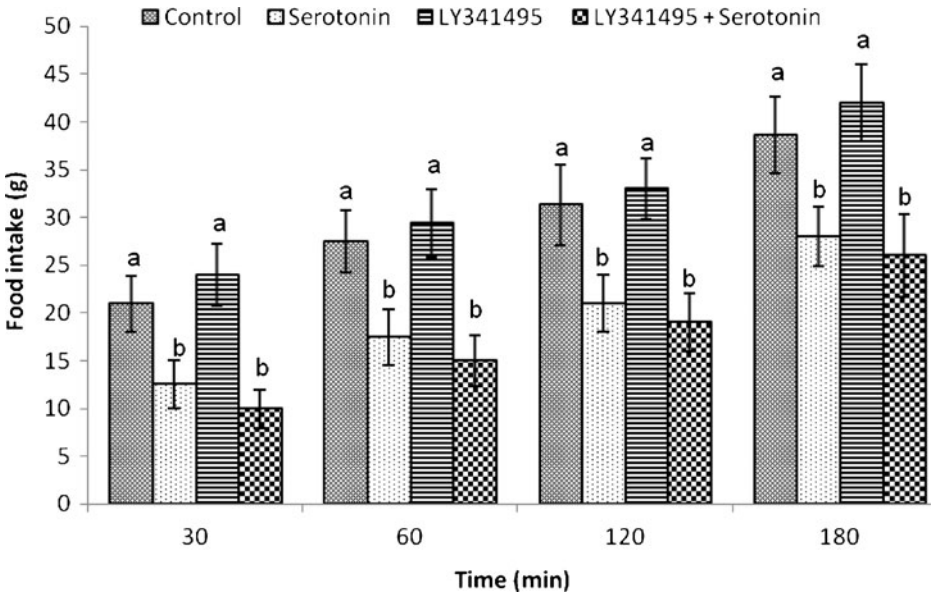

Fig. 4 Effect of ICV injection of LY341495 (150 nmol) followed by serotonin (10 μg) on food intake in 3-h food deprived chickens. Data are presented as mean ± SEM. Different letters (*a* and *b*) indicate significant differences between treatments ($P<0.05$)

In experiment 7, pretreatment with 20 ng CGP54626 had no effect on the hypophagia induced by 5-HT in FD3 chickens ($F_{3,\ 25}=2.65$) ($P>0.05$) (Fig. 7). In addition, CGP54626 (20 ng) alone had no effect on food intake ($F_{3,\ 25}=0.17$) ($P>0.05$) (Fig. 7).

Discussion

The present survey was a novel study which designed to reveal the possible modulatory role of 5-HT in glutamate and GABA mechanisms involved in feeding behavior in chicken. According to the results obtained from experiments 1–7 (Figs. 1, 2, 3, 4, 5, 6, and 7), 5-HT decreases food intake in FD3 chicks which was in agreement with our prior study on ICV injection of 5-HT; caused a significant decrease in food intake in Leghorn chickens deprived of food for 24 h (FD24) (Zendehdel et al. 2012a, b).

Ciranna (2006) suggested that 5-HT has modulatory effect on both excitatory and inhibitory responses mediated by glutamate and GABA respectively, and this interaction described in several CNS regions, especially in those controlling cognition and nociception. In experiment 1 the inhibitory effect of 5-HT on food intake was decreased by MK- 801 (NMDA receptor antagonist) (Fig. 1). In experiment 2, hypophagic effect of 5-HT was significantly attenuated by administration of CNQX (AMPA/Kainate receptor antagonist) in FD3 chickens (Fig. 2). It is claimed that 2 third of 5-HT ergic raphe

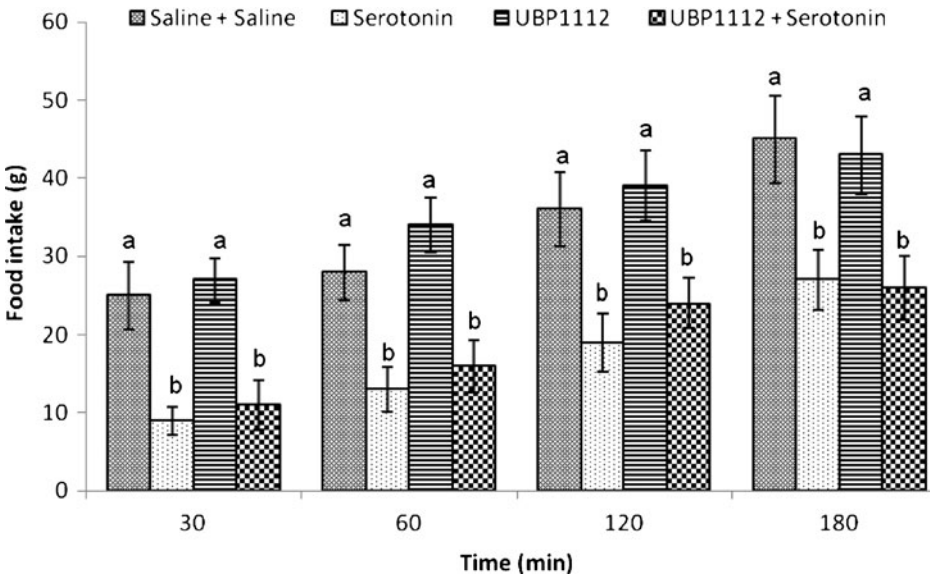

Fig. 5 Effect of ICV injection of UBP1112 (2 nmol) followed by serotonin (10 μg) on food intake in 3-h food deprived chickens. Data are presented as mean ± SEM. Different letters (*a*, *b*) indicate significant differences between treatments ($P<0.05$)

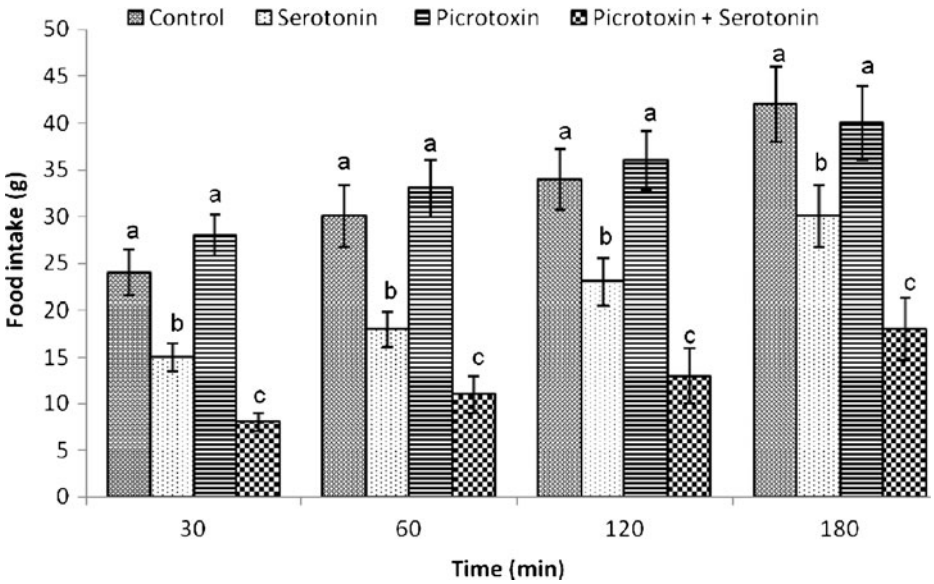

Fig. 6 Effect of ICV injection of Picrotoxin (0.5 μg) followed by serotonin (10 μg) on food intake in 3-h food deprived chickens. Data are presented as mean ± SEM. Different letters (*a*, *b* and *c*) indicate significant differences between treatments ($P<0.05$)

neurons use glutamate as a co-transmitter which they acts via AMPA/kainate-mediated excitatory post synaptic potentials (EPSPs) (Ciranna 2006). Based on obtained results, a possible interaction seems to be exist between 5-HT ergic and glutamatergic systems involved in feeding behavior in chickens and 5-HT exerts its modulatory effects through interaction with NMDA and AMPA/Kainate receptors. It has been reported that 5-HT enhances both NMDA- and non-NMDA-mediated effects in ventrobasal thalamus neurons (Eaton and Salt 1989). In this regard, one of the earliest observations on modulation of glutamate transmission by 5-HT in hippocampus showed that, the effects mediated through NMDA and 5-HT2 receptors converge via the same signal transduction mechanism (phosphatidylinositol breakdown) (Gandolfi et al. 1990). Accordance to these findings and our results, it seems 5-HT may have enhancement effects on NMDA and non-NMDA receptors in hypothalamus similar to description in ventrobasal thalamus and perhaps mediates its effect using similar convergence signal transduction mechanism as mentioned. However, it seems further investigations needs to clarify direct mechanism.

In experiments 3, 4 and 5 pretreatment with AIDA (mGluR I receptor antagonist), LY341495 (mGluR II receptor antagonist), and UBP1112 (mGluR III receptor antagonist), had no effect on the hypophagia induced by 5-HT in FD3 chickens (Figs. 3, 4, and 5). Previously reported, that LY341495 (mGluR2/3 antagonist) decrease food intake in rats (Semenova and Markou 2007). In contrast, it has been demonstrated that glutamate probably attenuates food intake via ionotropic and metabotropic receptors in broiler cockerels

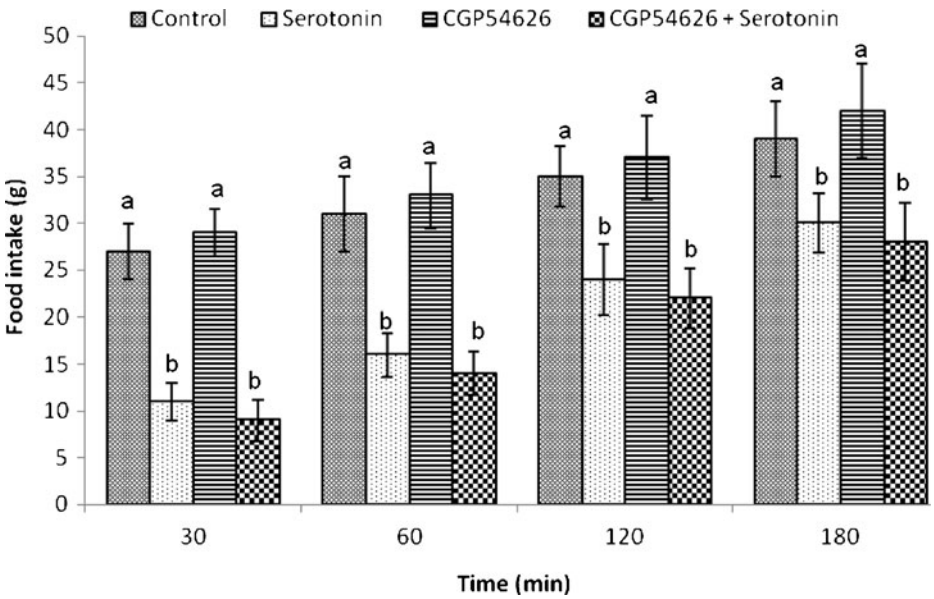

Fig. 7 Effect of ICV injection of CGP54626 (20 ng) followed by serotonin (10 μg) on food intake in 3-h food deprived chickens. Data are presented as mean ± SEM. Different letters (*a* and *b*) indicate significant differences between treatments ($P<0.05$)

(Baghbanzadeh and Babapour 2007). In comparison to our findings, it seems effect of glutamate on metabotropic receptors (mGluR I, mGluR II, mGluR III) cannot be modulated by 5-HT in broiler cockerels at least.

Scientists have found that the ICV injection of muscimol, a $GABA_A$ receptor agonist, increased food consumption in layer strain hens (Bungo et al. 2003) and broilers (Jonaidi et al. 2002; Tajalli et al. 2006; Zendehdel et al. 2008, 2009). Likewise, picrotoxin administration, a $GABA_A$ receptor antagonist, decreased food intake in chicks. It suggests a stimulatory effect of $GABA_A$ receptors on food intake in poultry (Jonaidi et al. 2012). In experiment 6, the inhibitory effect of 5-HT on food intake was amplified by picrotoxin pretreatment in FD3 chickens (Fig. 6) that shows possibly modulatory role of 5-HT on GABAergic neuron is exerted through interaction with this receptor.

Martın-Ruiz et al (2001) reported that more density of 5-HT1A and 5-HT2A receptors has been identified in prefrontal cortex (PFC) of pyramidal neurons, GABAergic interneurons, and axon terminals. Additionally, GABAergic interneurons are enriched in 5-HT2A receptors (Martın-Ruiz et al. 2001). It has been detected that GABA-mediated inhibitory transmission can be modulated by 5-HT and 5-HT- glutamate interactions in CNS (Ciranna 2006). Several lines of evidence suggest pointed that 5-HT2 receptors modulate post-synaptically $GABA_A$- mediated effects in pyramidal neurons from PFC (Martın-Ruiz et al. 2001). In addition, postsynaptic 5-HT2A receptors are abundant in apical dendrites and GABAA receptors are distributed on postsynaptic domains of GABAergic synapses on the soma and proximal dendrites (Yan 2002). It is reported that 5-HT2A and GABAA receptors in 5-HT ergic cell firing are mediated by M100907 and picrotoxinin (Martın-Ruiz et al. 2001).

In fact, 5-HT2 receptors, promote phosphorylation of $GABA_A$ receptors by activation of protein kinase C (PKC) and its anchoring protein RACK1 (receptor for activated C kinase), which leads to reduce $GABA_A$-mediated Cl-currents (Feng et al. 2001; Yan 2002). Considering this data and our findings, it seems 5-HT probably attenuates increased food intake-mediated by $GABA_A$ receptors through activation of protein kinase C mechanism as mentioned above. Indeed, there were no similar researches to compare our results with them.

In this regard, baclofen, a $GABA_B$ agonist, increased food consumption in layer- type hens (Bungo et al. 2003) whereas it had no effect in broilers (Jonaidi et al. 2002; Bungo et al. 2003). In agreement, microinjection of baclofen into the nucleus accumbens shell increased food intake in rats (Ward et al. 2000). In experiment 7, pretreatment with CGP54626 ($GABA_B$ receptor antagonist) had no effect on the hypophagia induced by 5-HT in FD3 chickens (Fig. 7). According to our data, hypophagic effect of 5-HT cannot be modulated by $GABA_B$ receptors in broiler cockerels. The current results highlight differential modulation between GABAA and GABAB receptors effects on food intake controlling in broiler cockerels. In mice, baclofen increased 5-HT release during the light but decreases it in the dark period (Takahashi et al. 2010). In addition, it is reported there are different sensivity to baclofen between presynaptic and postsynaptic GABAB receptors in mice which presynaptic receptors are much more sensitive to low doses of baclofen than the postsynaptic (Takahashi et al. 2010). We think it can be one of the reasons for difference effects of baclofen on food intake among layer and broiler strains but to our knowledge we think further researches need to identify differences in birds.

In conclusion, based on previous studies and our findings in this study, it seems 5-HT induced hypophagia can be modulated by glutamatergic and GABAergic systems in central regulation of food intake in chicken. Moreover, this modulatory effect is exerted through interaction of 5-HT with NMDA and AMPA/Kainate (and not mGluR I, mGluR II, mGluR III) receptors in cockerels. Our data also shows 5-HT as a modulator interacts with $GABA_A$ (and not $GABA_B$) receptors in poultry. Furthermore, it is described that modulatory mechanism of 5-HT over glutamate- and/or GABA-mediated transmission has a key role in circadian rhythms regulation (Ciranna 2006) which we think can be linked to food intake controlling mechanism. Finally, the authors recommend merit further investigation need to clarify direct interaction of gutamatergic and GABAergic systems on 5-HT- induced feeding behavior in chicken. Also, it seems more researches needs on other physiological systems to clarify physiology of food intake regulation in poultry.

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