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Food Intake Regulation in Birds: the Role of Neurotransmitters and Hormones

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Abstract

BACKGROUND: Neurotransmitters (NTS) are endogenous chemicals secreted from neural terminals into the synaptic cleft of the chemical neurons in order to affect their receptors. NTS play vital physiological role as stimulatory, inhibitory or modulatory compounds.

OBJECTIVES: This review was aimed to summarize the roles of the most important NTS which regulate food intake in the avian species.

RESULTS: Over 40 neurotransmitters are known as regulatory agents that control ingestion behavior in mammals and birds. Acetylcholine (Ach), epinephrine (EP), norepinephrine (NEP), histamine, gamma amino butyric acid (GABA), glycine, serotonin and glutamate have been identified as the mediatory agents about regulation of feeding behavior in birds. Based on the molecular weight and the type of efficacy, NTS have been categorized into the two main groups including "the small molecular weight fast-effective NTS and the large molecular wieght slow-effective neuropeptides. Various physiological functions have been presented for NTS and it seems many other unknown effects and even possible interactions among them are still questionable. Appetite control, mediatory role of ingestion behavior and regulation of food intake have recently been highlighted among various roles of NTS in chicken.

CONCLUSIONS: Food intake regulation is a complex physiologic process that is under the control of the central and environmental signals. Considering of the involvement of feeding behavior in other major physiological processes such as the growth, immunity and production, it is necessary to realize the role of different mediators which are affecting and modulating food intake in avian species.

KEYWORDS: Appetite, Bird, Food intake, Neurotransmitter, Nutritional behavior

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Introduction

Neurotransmitters (NTS) are endogenous chemicals that are released by neuronal terminals and affect other neural membranes at the synaptic cleft. NTS play different stimulatory, inhibitory and/or modulatory roles in the Central Nervous System (CNS) to regulate various physiologic behaviors such as perception, pleasure, excitement, memory, learning and etc. Acetylcholine (ACh) is known as the major neurotransmitter that plays a role at the neuromuscular junction (NMJ). ACh, has been discovered in 1945, was the first known chemical messenger. Now it is well described that ACh has major physiological functions in the CNS and in the Peripheral Nervous System (PNS) (Koeppen and Stanton, 2017). Chemical messengers known as NTS are responsible to transfer impulses in the chemical synapse, unlike the electrical synapse that is related to cellular cytoplasm. Based on the molecular weight, NTS have been categorized into small weight molecule, peptide and gas NTS. Ach, amino acids, biogenic amines and purines have been considered as the small molecules. The production site of peptide NTS or neuropeptide is presynaptic terminal, while regular ones are synthesized in the cell body of the neurons (Hall, 2015; Koeppen and Stanton, 2017). Regular NTS pack inside the synaptic vesicles and are released by exocytosis, while the gas ones are synthesized following the depolarization of the neuron and then are released by simple diffusion as highly permeable substances (Koeppen and Stanton, 2017). Regulation of food intake in mammals and birds is a complex mechanism that depends on integration of internal and external signals received by the CNS. CNS and especially the hypothalamus play key role in appetite control in birds same as mammals. Peripheral signals such as hormonal ones usually originate from gastrointestinal (GI) tract or liver. These signals can enter the CNS and influence the food intake (Denbow, 1994). It should be considered that chicken's crop does not directly affect the feeding behavior but mediatory receptors present in this area can indirectly regulate food intake. It seems, physical restriction like crop enlargement probably limits food consumption in birds. Moreover, the hypothalamus as the major center receives and integrates impulses that come from the GI tract, pancreas, liver and adipose tissue besides central signals come from the brain. It has been considered that physiological condition can affect appetite via alteration of the orexigenic and anorexigenic NTS' level. That's why NTS have been supposed as a communication bridge between peripheral and central signals that lead to appetite centers (Denbow, 1994). The central and peripheral stimulators integrate in the brain centers and finally lead to inhibition or stimulation of ingestion.

Among all of the NTS that are involved with the food intake regulation regulation, epinephrine (EP), norepinephrine (NEP), dopamine, serotonin and histamine belong to the subgroup of biogenic amines, while gamma amino butyric acid (GABA) and glutamate are amino acid and neuropeptide Y (NPY) and opioids are recognized as neuropeptides. Considering the importance of food intake in several physiological processes such as growth, immunity and production, realizing the role of NTS on ingestion behavior has been one of the interesting fields of research within the last decades. This study attempted to collect and discuss the roles of various NTS and their interaction in regulation of food intake in avian species.

Feeding behavior in birds, a comparison between mammals and birds

Our knowledge about the food intake regulation of food intake in mammals and birds has been increasing during the last decades. It seems similar regulatory procedures to mammals are active in birds too. Various NTS and their receptors are major players in regulation of appetite, energy expenditure and weight gain in mammals. It should be considered that most of the same NTS in mammals have been identified in the avian brain too. It is worthy to know that several differences are highlighted between two species. For instance, it has been illustrated that the pancreatic peptide had a decreasing effect on food intake in mammals while in the same study, this peptide increased food intake in birds (Sturkie, 2012). Also, another study presented that ghrelin is the hyperphagic agent in mammals, while ghrelin has been known as the anorexic agent in birds (Cline and Furuse, 2013). In addition, several peptides such as melanin-concentrating hormone (MCH), orexin A and B are known as orexigenic agents in mammals, but they do not alter food intake in birds. Although the reasons behind such contradictory observations is still ambiguous, it seems the higher metabolism rate, general adaptation for flying and having beak, feathers and unique GI tract, respiratory systems as well as light bone and short colon could imply different records about NTS function in birds in comparison with the other vertebrates (Tachibana and Tsutsui, 2016).

Hypothalamus as the key place in food intake regulation and appetite control

Hypothalamus is the most important center for integration of central and peripheral signals that lead to the CNS to affect food intake. Arcuate nucleus (Arc) and paraventricular nucleus (PVN)of hypothalamus, lateral hypothalamic area (LHA) and medial hypothalamus area (MHA) are the major parts of the hypothalamus involved in the control of body weight. Like mammals, lesioning in the MHA increased food intake whereas lesioning in the LHA decreased food intake in birds (Kuenzel et al., 1999). Although these regions were traditionally considered as the satiety and hunger centers respectively, it is currently believed that they are part of a larger neural circuit involved in ingestion in brain. What is well noted is that the CNS has a key role in metabolism, growth and appetite control in avian species. Based on the transcriptomics studies, several genes have been discovered in birds that all of them are related to the ingestion behaviors. For example, expression of a gene that is responsible for glucose transfer in the brain has been changed during migration and non-migration seasons (Jones et al., 2008). A microarray analysis study on hypothalamic genes which control metabolic function in birds such as thyroid hormone deiodinase-2 and proopiomelanocortin (POMC) revealed that in food-deprived chicken, expression of these genes has been altered (Higgins et al, ., 2010).

Neurotransmitters, key regulatory agents in ingestion behavior

Peptide NTS and Hormones

A.1. Neuropeptide Y (NPY)

The NPY is one of the most abundant peptide in the CNS which influences food intake and appetite. Structurally, NPY consists of 36 amino acids with a single different residue between mammalian and avian amino acid sequences. NPY gene controls food absorption (Kuenzel and Fraley, 1995) and reproductive activity. NPY is the most potent orexigenic peptide which functions through Y2 and Y5 NPY receptors. It is well presented that Arc is the primary center for regulation of food intake at the hypothalamus in mamalian. It has been shown that the Arc is almost permeable to NPY and could receive peripheral inputs from lateral ventricle fluid. It has been indicated that the first order orexigenic neurons that are located in the Arc are responsible for NPY secretion. Hyperphagic effect of NPY in broiler and leghorn pullet was reported in studies by Denbow et al. (1988) and Cline and Furuse, (2013), respectively. Recently, Chen et al. (2016) demonstrated that ICV injection of NPY in neonatal chicken was associated with food intake increment, while injection of antibody against NPY reduced food intake in early hatched chickens. Mediatory role of NPY and related receptors NPY1/NPY2/NPY5 about regulation of food intake in birds has been recently documented by other scientists (Yousefvand et al., 2018 & 2019) while the underlying mechanism in birds is not clear yet.

A.2. Melanocortin

Melanocortin is derived from a larger protein called proopiomelanocortin (POMC). In mammals, melanocortin mainly releases in the Arc and it seems that the chickens' POMC gene is structurally similar to other vertebrates. Melanocortin has five receptors called MC1R-MC5R that are all distributed throughout the body but MC3R and MC4R are more abundant in the brain (Sturkie, 2012). Mammalian melanocortin system plays a key function in control of nutritional behavior. It has been shown that injection of MC3R receptor agonist could reduce food intake in mice. In addition, ICV injection of melanocyte stimulating hormone (MSH) which is derived from POMC, reduced food intake in food-deprived broilers (Kawakami et al, 2000). Besides, modulatory effect of MC3R and MC4R on serotonin-induced food and water intake of broiler cockerels has been documented by Zendehdel et al.(2012).

A.3. Opioids

Opioids are primarily known as inhibitory NTS. Presence of four opioid receptor types (delta, kappa, mu and NOP) has been documented in the avian species (Gallus gallus) (Dreborg et al., 2008). Opioid receptors are widely distributed throughout the CNS and they are highly expressed in several areas which are involved in regulation of food intake such as hypothalamus, Nucleus accumbens, amygdala and nucleus tractus solitarius. It has been indicated that opioidergic system is associated with pain perception, respiratory and immune system activity. Riters (2011) showed opioidergic systems' effect on feeding and sexual behaviors in chicken. It has been postulated that opioids are exerting their effects mainly by binding to the μ and κ receptors. It is mentioned that administration of opioid antagonist such as naloxone and naltrexone has reduced food intake in both broiler and layers (Denbow, 1999). Also, Bungo et al. (2005) reported that administration of μ receptor antagonist, especially the μl decreased hyperphagic effect of NPY in broiler. In this study, it was revealed that β-funaltrexamine a μ-opioid antagnist, decreased hypophagic effect of D-Ala2, N-Me-Phe4, Gly-ol-enkephalin (DAMGO) and ICV injection of μ-opioid agonist reduced food intake in broilers, while two hours post injection of μ and δ agonists, food intake increased. In addition, Shojaei et al. (2015) showed that ICV injection of DAMGO a μ-opioid receptor agonist, decreased cumulative food intake in 3 hours food-deprived (FD3) neonatal Bovans chickens, while administration of [D-Pen^2,D-Pen^5]enkephalin (DPDPE) a δ-opioid receptor agonist and U50488H a κ-opioid receptor agonist, enhanced food intake. Recently, Zendehdel et al. (2016) demonstrated that ICV co-injection of DAMGO and SCH23390 a D1 like receptor antagonist, diminished DAMGO-induced hypophagia in chickens. It was the first time that a functional interaction between opioidergic and dopaminergic systems about food intake regulation had been reported in birds.

Based on another study, in physiologic condition, prostaglandin D2 (PGD2) and NPY might regulate feeding behavior. It has been shown that ICV injection of naltrindole a δ-opioid receptor agonist, activated cyclooxygenase-2 (COX-2) and produced PGD2 which in turn could stimulate release of NPY and appetite accordingly (Kaneko et al., 2012). This finding has been indicated that appetite stimulating role of δ-opioid receptor is most likely mediated through activation of the PGD2-NPY pathway.

A.4. Ghrelin

As an endogenous ligand for growth hormone (GH), ghrelin was isolated from rat and human's stomach about 15 years ago. It has been shown that ghrelin as one of the most important appetite regulating peptides has stimulatory effect on food intake and release of GH in the brain. Gene expression of ghrelin and its receptor GHS-R1a in the hypothalamus, proventriculus, liver, and abdominal fat of chicken's body has been measured recently. In is worthy to note that expression of ghrelin and GHS-R1a could alter because of feeding status and dietary energy level (Song et al., 2019). Although ghrelin is known as a stimulant factor for secretion of human and avian GH in brain but it has been recorded that food intake has been strongly inhibited by ghrelin in birds (Kaiya et al., 2011). Another study confirmed the hypophagic effect of ICV injection of ghrelin in avian species (Taati et al., 2011; Zendehdel et al., 2013). While ghrelin could stimulate NPY secretion at the Arc neurons in rat and could induce hyperphagia in mammals, despite the underlying mechanism for hypophagic effect of ghrelin in birds is not clear yet. It must be noted that in one study co-injection of ghrelin with NPY could inhibit hyperphagic effect induced by NPY in birds (Furuse et al., 2007).

A.5. Leptin

Leptin is a small (16kDa) peptide hormone released from adipose tissue and it has been known as a product of obesity gene that is released from adipose tissue. It has been indicated that central and systemic injection of leptin has reduced food intake and enhanced energy expenditure. By affecting the CNS, leptin has an important role about ingestion behavior (Valassi et al., 2008). Chicken's leptin cDNA (cLEP) (Genebank AF 012727, AF082500) was cloned and sequenced in birds and it is more than 90% orthologous to murine one. Sequencing of leptin gene in chicken has confirmed the presence of 145 amino acids instead of 146 amino acids in mammals. It is noted that the presence of leptin was proposed in chicken even before sequencing of leptin in this species (Ashwell et al., 1999) however, there were controversial reports about missing (Hron et al., 2015; Lovell et al., 2015) or existence of cLEP sequence in chicken genome for almost a decade till Farkašová et al. (2016) showed the presence of the LEP gene in birds. Whereas, there was no controversy about expression or non-expression of avian leptin receptor in chicken (Richards and Poch, 2003). Same as mammal, suppressive effect of ICV injection of human leptin on feeding behavior in neonatal chickens has been confirmed by Denbow et al. (2000). Interestingly, ICV injection of mouse leptin did not influence chicken's feeding behaviors. These findings confirmed variation between leptin's action in different avian species and between birds and mammals (Bungo et al., 1999) which could be because of variation of the leptin genes among avian strains and between different species (Boswell and Dunn, 2015). Based on the literature, at least a part of leptin which affects feeding behavior has been exerted through the available neurologic pathway which is the connection between leptin and melanocortin system. In this regards, it is well presented that leptin could stimulate α-MSH, MCR3, and MCR4 agonist activity and is able to inhibit Agouti related peptide (AgRP), MCR3 and MCR4 antagonist activity (Dridi et al., 2005).

Biogenic amines

Biogenic amines are small molecules which are synthetized in the cytosol of the pre-synaptic terminals and are packaged inside the neural vesicles. When the neurons are depolarized, these vesicles release their contents into the synaptic cleft. Cell bodies of the mentioned neurons are mainly located in the brain stem. For instance, noradrenergic neurons which are located in the brain stem and locus coeruleus, as well as dopaminergic neurons which are located inside the substantia nigra (SN) at the midbrain (Hall, 2015).

B.1. Serotonin (5-hydroxytryptamine), 5-HT

5-HT is a monoamine neurotransmitter and is synthesized in process of hydroxylation and decarboxylation of tryptophan. Neurons located in the raphe nuclei are distributed through the brain stem and the reticular formation (Furuse et al., 2007) are the major production source for serotonin inside the brain. Effects of serotonin on food intake has been demonstrated in several species (Ganong and Ganong, 1995). In addition to the feeding behavior, serotonin regulates various CNS functions such as sleep, muscle contraction, memory and learning (Furuse et al., 2007). Also, the role of serotonergic system related with feather pecking (FP) and behavioral modulations related to FP, such as feather eating, foraging, anxiety and activity have been studied and indicated by several researchers (Kops et al., 2014). There is evidence that serotonin especially in mammals-had anorexigenic effect. In this regard, Zendehdel et al. (2012) demonstrated that ICV administration of serotonin has diminished food and water consumption in three week -old cockerels, while serotonin was not able to change food intake in chickens younger than one week-old. In addition, it has been well documented that some neurotransmitters affect CNS behavior like ingestion by interaction with other central systems. For instance, Shojaei et al. (2015) for the first time reported available interaction between opioidergic and serotonergic system in layer-type chickens because ICV co-injection of parachlorophenylalanine (PCPA) and DAMGO inhibited hypophagic effect of DAMGO. In this study authors suggested that the influence of μ-opioid receptor on food intake is most likely mediated through interaction with the serotonergic system. However, ICV injection of PCPA as a brain serotonin depletive factor and SB242084 as a 5-HT2C receptor antagonist did not affect appetite in neonatal layer type chickens (Yousefi et al., 2019). Although the reason behind these contradictory results is not fully understood, it seems the age of birds in study could be a possible underlying factor for different observations in the mentioned study. Besides, it has been postulated that age-dependent physiological changes can affect expression of neuropeptide receptors and consequently these changes could result in variation in chicken's response to the administrated compounds. For example, in a recent study, Zendehdel et al. (2017) suggested that serotonin-induced feeding behavior is probably mediated via α2 and β2 adrenergic receptors in neonatal layer-type chicken. In addition, interaction between N/OFQ and the serotonergic system (via 5-HT2C receptors) on food intake in chickens has been documented by Zendehdel et al. (2013).

B.2. Histamine

Histamine known as a biogenic amine produced by histidine decarboxylase (HDC) enzyme in the tuberomammillary nucleus of the posterior hypothalamus with multifunctional action -not only as NTS but also as a neuromodulator agent- in the CNS and PNS of mammals and birds. Cloning of the HDC-cDNA demonstrated presence of this enzyme in chicken hypothalamus which has highly homologous sequencing to the mammalian counterpart (Bessho et al., 2014). Four G-protein receptors have been identified for histamine, including H1, H2, H3 and H4. It has been reported that endogenous histamine regulated feeding behavior through central H1 receptor in rat and poultry (Sakata et al., 1991). In this regard, ICV injection of chlorpheniramine as the H1 receptor antagonist, increased cumulative food intake in rodent and birds (Zendehdel et al., 2008). Previously, ICV administration of α-fluoromethylhistidine (α-FMH) -the histidin decarboxylase inhibitor- increased food consumption in chicken (Denbow et al.,2000). A suggested underlying mechanism for hypophagic effect induced by histamine is that NTS could stimulate POMC neurons and block the NPY pathway in the hypothalamus of both mammalian and bird species. In addition, it has been mentioned that there is a functional interaction between histaminergic system and cholecystokinin (CCK), a peptide hormone and satiety mediator, and histamine could reduce food intake in both of these species. Also, it has been already indicated that the H3 is the histaminergic receptor involved in hypophagic effect induced by CCK. In this regard, it has been suggested that in addition to the direct effect of CCK on its receptor (CCK-A), CCK also could induce satiety by stimulation of histamine release in brain (Attoub et al., 2001). It might be considered that the H3 receptor is an auto-receptor that inhibits endogenous histamine and is regulating HDC and histamine synthesis. In this study showed that ICV injection of thioperamide as H3 antagonist enhanced delivery of histamine in the CNS and could cause higher food consumption in three-week old broilers. In another recent study, mediatory role of H1 histamine receptors on lipopolysaccharide (LPS) induced hypophagia has been illustrated (Zendehdel et al., 2016). Furthermore, mediatory role of central histaminergic receptors on other neural systems such as noradrenergic system and oxytocin-induced ingestion behavior has been recently presented (Mirnaghizadeh et al., 2017). Also, interplay of H1/ H3 receptors on feeding behavior induced by nesfatin-1 has been studied and approved by Heidarzadeh et al. (2018).

Catecholamine: Dopamine, EP and NEP known as catecholamine because they have a common synthesis pathway and all are driven from tyrosine amino acid.

C.1. NEP and EP

NEP and EP play a critical role to make physiological homeostasis and normal mental behaviors in response to the stressful stimuli in chicken. Based on the literature, mediatory role of catecholamines to regulate food consumption highlighted their effects on birds' production and welfare implications. In addition, vital regulatory activity of EP and NEP in brain-gut-microbiome axis has emphasized the importance of adrenergic system in chicken (Dennis et al., 2016). Neuroanatomical studies about these mediators have revealed that noradrenergic fibers entered the solitary nucleus at the medulla oblongata. These fibers have been shown as essential factors for regulation of food intake in rat. Although ICV injection of EP increased food intake in chicken (Denbow et al., 1981), same treatment in turkey showed controversial result and interestingly, the same study in leghorn did not influence food intake in this strain (Denbow et al., 1983). Based on Denbow and Sheppard's. (1993) report, variation of the NEP injection sites affected birds' food intake response same as what has been already reported in mammals. For example, it has been shown that ICV injection of NEP in the ventromedial nucleus of hypothalamus, PVN and the medial septal nucleus stimulated feeding behavior. While, injection at the nucleus reticularis, superior part of pars dorsalis and tractus occipitomesencephalicus inhibited food intake in layer-type chickens (Denbow and Sheppard, 1993). Also, Katayama et al. (2010) demonstrated that ICV injection of high dose of NEP did not modulate mRNA expression of NPY and POMC in broilers and that is why food-regulating effect of the NEP is independent from the NPY and the POMC pathway. Furthermore, Zendehdel et al. (2014) showed that ICV pretreatment with the β2 receptor antagonist could attenuate hypophagic effect of ghrelin in cockerels and suggested that the effect of ghrelin on cumulative food intake is mediated via β2 adrenergic receptors.

C.2. Dopamine

Dopamine is an important neurotransmitter in the CNS and has various functions in the body such as perception, excitement and food intake regulation. Dopamine is significantly distributed in nucleus accumbens, amygdala, and hippocampus. It has been considered that dopaminergic and serotonergic system formed collaboration circuit called the 5-HT-DA neural which has a critical role in regulating brain behavior and maintaining mental health in chicken (Huang et al., 2019). Regarding ingestion behavior for the first time, Zendehdel et al. (2014) demonstrated that following stimulation of D1 receptor in brain, food intake has been increased in broiler-type chicken. However, it seems that the D3 and D4 dopamine receptors are not involved in food intake control in birds while D2 even has mediatory role on food intake regulation induced by cannabinoid system in layer-type chickens (Khodadadi et al., 2017). Besides, Hashemzadeh et al. (2018) showed an available interplay between D1 dopaminergic and GABAA receptors about regulation of food intake in birds. Also, the mediatory function of D1 and D2 receptors on feeding behavior induced by other central systems has been confirmed by Zendehdel et al. (2019) and Mahzouni et al. (2016).

Amino acid neurotransmitters and gaseous molecule:

D.1. Glutamate

Glutamate is the major stimulatory neurotransmitter present at synapse in the CNS. There are two families of glutamate receptors known as ionotropic glutamate receptor (iGuR) such as N-Methyl-D-aspartic acid (NMDA) and α-amino-3-hydroxy-5-methyl-4-isoxazolepropionic acid (AMPA) and metabotropic receptors including mGluRI, mGluRII and mGluRIII. Paperna et al.

(1996) showed that all glutamate receptors are almost homologous to the mammalian ones and presented in the brain. It has been reported that ICV administration of glutamate or glutamate agonist into the LH suppressed food consumption in cockerels (Baghbanzadeh and Babapour, 2007). Recently, it has been shown that the influence of glutamate on feeding behavior was mostly mediated via NMDA and AMPA receptors while stimulation of metabotropic receptors did not alter food intake in birds (Mortezaei et al., 2013). It should be considered that the mediatory role of glutamatergic receptors such as NMDA and AMPA receptors about regulation of food intake induced by other neural systems in birds have been clearly presented by other researchers (Zendehdel et al., 2012; Ahmadi et al., 2017; Keyshams et al., 2017).

D.2. Gamma-Aminobutyric acid (GABA)

GABA is a glutamate-driven neurotransmitter. The enzyme glutamic acid decarboxylase (GAD) that catalyzes synthesis of GABA is expressed in GABAergic neurons. It is a major criteria to recognize GABAergic neuron in brain. GABA is the main inhibitory neurotransmitter in the CNS. The striatum and purkinje cells of brain cortex are the most important centers that express GABAergic neurons (Koeppen and Stanton, 2017). GABAergic receptors are known as GABAA, GABAB and GABAC. GABAA and GABAC are ligand-gated ion channel whereas GABAB is a G-protein receptor. Based on a previous study, hypothalamic neurons showed mammalian-like responsiveness to the GABA administration and especially GABAB receptor is involved in hypothalamis response to leptin in neonatal chickens (Bogatyrev et al., 2017). It has been reported that ICV injection of GABAA agonist has amplified food intake in layer and meat-type cocklers. Moreover, ICV injection of GABAB agonist enhanced cumulative food intake in rat and layer-type chickens, but did not affect food intake in broilers (Zendehdel et al., 2009). However, GABAA is known as hyperphagic agent in meat-type chickens (Jonaidi et al., 2002). Based on this information, it seems GABA-induced feeding behavior in birds is somehow different in terms of genetic variation. It is necessary to mention that the broilers have higher food consumption rate, metabolism rate and energy expenditure (Saneyasu et al., 2011) in comparison with layers. Genetic background might be a notable reason to justify the different obtained results from studies on broiler and layer-type chickens when we are studying the same pathways in different strains.

D.3. Nitric oxide

Nitric oxide is a somewhat new identified neurotransmitter. Nitric oxide is a gaseous molecule which is synthesized during the oxidation of arginine to citrulline. This reaction is catalyzed by nitric oxide synthase. It was previously shown that ICV injection of L-arginine decreased food consumption, whereas L-NAME (L-Nitro Arginine Methyl Ester) as a nitric oxide synthesis inhibitor, enhanced cumulative food intake in chickens (Choi et al., 1994). Furthermore, co-injection of L-NAME and gaboxadol could amplify the appetizing effect of gaboxadol in neonatal layer-type chickens. There is evidence that nitric oxide has a mediatory role about opioid-induced feeding behavior in birds (Hassanpour et al., 2015; Alimohammadi et al., 2015). In addition, it has been shown that ICV administration of L-arginine decreased mRNA expression of the glutamic acid decarboxylase (GAD 1 and 2) genes (Mokhtarpouriani et al., 2016).

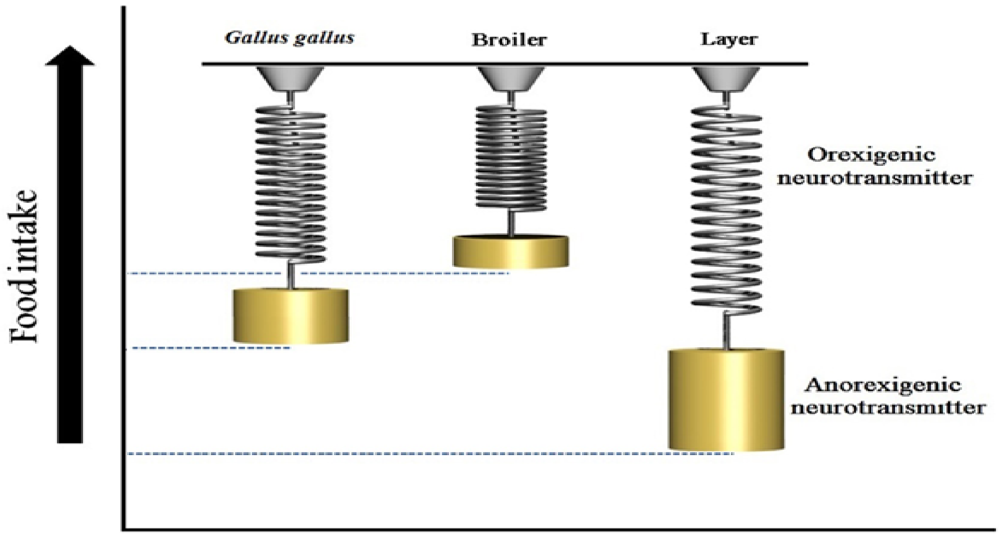

Figure 1. A simple model for description of the food intake differences between broiler and layer- type breed in comparison with their ancestor (Gallus Gallus). Springs indicate the effect of orexigenic neuropeptide and hanging masses are the total amounts of anorexigenic neuropeptides. Different responses of both strains to ICV injection of mediators showed that the genetic selection for the production of more meat or egg has altered the response of brain to neuro-chemical compounds in comparison with their ancestor, which is a reflection of appetite regulation mechanisms.

Cannabinoids

Cannabinoid is a marijuana (Δ9-tetrahydrocannabinol) active component which is a psychoactive ingredient. Endocannabinoid system (ECS) is consisted of the endogenous lipid-based retrograde neurotransmitters that bind to cannabinoid receptors. What makes cannabinoid different from the other regular ones is that endogenous cannabinoids are not stored in synaptic vesicle and act as retrograde messengers inside the brain. Expression of CB1 and CB2 as major and abundant cannabinoid receptors in the brain of birds has been previously approved by scientists. While CB2 receptor is generally present in peripheral tissue and mostly involved in immune system of mammals. There are several endogenous ligands for cannabinoid receptors such as 2-arachidonoylglycerol and anandamide compounds. Stimulating effect of 2-arachidonoylglycerol, as selective agonist of CB1 receptor, on food intake in layer hens was documented by Zendehdel et al. (2015). In addition, Alizadeh et al. (2015) suggested that CB1 and CB2 receptors have an important role in ingestion behavior in FD3 neonatal layer-type chicken. This finding was confirmed in a study done by Khodadadi et al. (2017) when they were studying the mediatory role of D2 dopaminergic receptor on food intake induced by CB1 and CB2 agonist.

Discussion

Neural pathway of food intake regulation and energy balance consists of various central NTS systems mostly interact with each other at the CNS stage. During the last decades, genetic selection of avian breeds just to achieve higher meat and egg production has been associated with the major changes in central pathways of the appetite regulation. As broiler-type chickens have been selected to grow fast and the layer hens have been selected for higher egg production procedure, layer hens should have lower weight in comparison with the meat-type chickens (Fig. 1). There are not only considerable differences about regulation of food intake between mammals and birds but also different strains of bird showed variations in the central pathway that regulate ingestion behavior. Author attempted to summarize revealed information about the most important NTS that are involved in food intake regulation with focus on avian species. The hypothalamus, as a complex neural network, is the major location of hyperphagic and hypophagic pathways. Nutritional behaviors are complex processes consisting of various aspects of food consumption such as food searching or hunting, stimulation and even food selection. Although numerous investigations have been performed to clarify roles of various related NTS, more studies are needed to reach deeper insight about NTS' characteristics and available interactions between them which affect feeding behavior. It has been widely accepted that the hyperphagic peptides have greater impact on food intake. To identify underlying mechanisms in mammals and birds, several conditions such as calm or stressful environment and food deprivation prior to initiation of the experiment or change of diet type (in terms of change in taste) should be considered when we are analyzing NTS' activity. Nowadays growing population and increasing demands for meat and eggs as global food concern put emphasis on poultry industry and chicken breeding. That is why any information about effective factors which are increasing poultry food intake in broiler-type chickens and maintenance of ideal total body weight in layer hens may lead us to reach a better understanding of the basic science of energy homeostasis in this valuable species and help nutritionists to improve poultry industry.

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Conflict of Interest

The authors declare that there is no conflict of interest.

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تنظیم دریافت غذا در پرندگان: نقش میانجی‌های عصبی و هورمون‌ها

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چکیده

زمینۀ مطالعه: میانجی‌های عصبی (نوروترانسمیترها) ترکیباتی هستند که از پایانه های عصبی نورون‌های شیمیایی به فضای سیناپسی ترشح می‌شوند و بر گیرنده‌های غشایی دیگر نورون‌ها اثر می‌گذارند.

هدف: مرور نقش برخی از میانجی‌های عصبی موثر بر تنظیم مصرف غذا در پرندگان و عوامل تعدیل کننده ی آنها می‌باشد.

نتایـــج: میانجی‌های عصبی می توانند به عنوان یک عامل تحریک کننده، مهارکننده و یا تعدیل کننده در تنظیم اخذ غذا در پرندگان و پستانداران نقش آفرینی کنند. تا کنون بیش از ۴۰ میانجی عصبی مهم کشف شده است که از آن جمله می‌توان به استیل کولین، اپینفرین، نوراپینفرین، هیستامین، گاما آمینو بوتیریک اسید (GABA)، گلایسین، سروتونین و گلوتامات به‌عنوان مهمترین میانجی های عصبی موثر بر کنترل رفتار تغذیه ای اشاره کرد. به طور کلی، میانجی های سیناپسی به دو دسته تقسیم می شوند، دسته‌ی نخست شامل مولکول‌های سبکی هستند که سریع الاثر می باشند. دسته دوم، نوروپپتیدهایی با وزن مولکولی بزرگتر می‌باشند و نسبت به دسته ی نخست، کندتر عمل می‌کنند.

نتیجه‌گیری نهایی: تاکنون اعمال فیزیولوژیک متنوعی برای میانجی های عصبی نشان داده شده است، اما به نظر می رسد هنوز سؤالات بسیاری درمورد اثرات ناشناخته و همچنین تداخل عمل احتمالی آن ها با یکدیگر وجود دارد. از مهمترین نقش هایی که برای میانجی های عصبی در نظر گرفته می شود، اثر آنها بر تنظیم اشتها و مصرف غذا است. تنظیم مصرف غذا فرآیند پیچیده ای است که بواسطه برهمکنش و تجمیع پیام‌های (سیگنال های) مرکزی و محیطی کنترل می‌شود. با توجه به اهمیت تنظیم اشتها دردیگر فرآیندهای فیزیولوژیک از جمله رشد، ایمنی و تولیدمثل، شناخت نقش میانجی های مختلف بر مصرف غذا و همچنین عوامل مؤثر بر تعدیل آنها اهمیت فراوانی دارد.

واژه‌های کلیدی:

اشتها، پرنده، اخذ غذا، میانجی های عصبی، رفتارهای تغذیه ای.

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