



Review

The endocrine control of energy homeostasis in chickens

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ABSTRACT

Energy homeostasis (balance) depends on the relationship between the amount of consumed feed energy and energy expenditure. Coordination of energy expenditure and feed intake (appetite) is necessary for the regulation of body composition. The hypothalamus integrates peripheral and central signals to generate satiety or hunger. Birds and mammals utilize common signaling molecules but some molecules possess different/opposite functions. If relevant, particular differences with the mammalian regulatory system are highlighted in this review. For example, obestatin had no significant effect on feed intake of chicks, but it was claimed to decrease food intake in mammalian species. Ghrelin displayed appetite-stimulating effects in mammals but appetite-decreasing effects in birds. Recently, the function of the hypothalamic AMPK signaling pathway on feed intake regulation has received considerable attention in poultry. Alpha-lipoic acid might exert its appetite-decreasing effect by the AMPK signaling pathway. This review discusses the central regulation of energy homeostasis, role of (an)orexigenic peptides, effect of feed deprivation on hypothalamic neuropeptide gene expression and provides a model for involvement of AMPK in the regulation of avian energy balance.

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1. Introduction

The energy balance is the net result of energy intake (appetite) on the one hand and energy expenditure on the other hand. Both the short term and long term regulation of energy homeostasis are mediated by (neuro) endocrine factors that affect appetite as well as energy expenditure. There is by far much more relevant information available on mammalian compared to avian species and on the central regulation of feed intake versus the central control of energy expenditure. With respect to the latter, the paraventricular neuropeptides corticotropin-releasing hormone (CRH) and thyrotropin-releasing hormone (TRH) seem to be involved in a similar way in mammals and birds (Richards, 2003). The present review focuses on the regulation of appetite in chickens with emphasis on some peculiar differences with mammals, the absence of any effects of obestatin and finally on recent work on the emerging role of the key regulator AMP-activated protein kinase (AMPK).

2. Role of central regulation

The control and regulation of voluntary food intake in animals and humans is very complex, involving brain-gut axis and hormonal and non-hormonal factors acting through the integration

by the hypothalamus. Several hypothalamic nuclei expressing (an)orexigenic neuropeptides play key roles in appetite regulation as well as in the control of energy expenditure. In avian species, the neuropeptide Y (NPY) neurons in the infundibular nucleus co-express agouti-related peptide (AgRP, an endogenous melanocortin receptor-4 antagonist) and hence stimulate food intake (Hahn et al., 1998). On the other hand, infundibular pro-opiomelanocortin (POMC) and cocaine and amphetamine-related transcript (CART) have anorexigenic properties. The above neuropeptides are used to be cataloged into first-order neurons (Morton et al., 2006). Candidate second-order neurons include those that express orexins and melanin-concentrating hormone (MCH) in specific hypothalamic nuclei and these peptides might also be involved in appetite regulation. It is suggested that this response is rather due to a stimulus from first-order orexigenic signals (NPY/AgRP) than from anorexigenic neuropeptides (POMC/CART) (Song et al., 2012a). CRH and TRH have also anorectic properties and stimulate energy expenditure (Hillebrand et al., 2002).

The hypothalamus integrates a vast array of signals from the periphery such as blood metabolites and digestive tract, reserve (fat) tissue and nervous (mainly n. vagus) signals. Hypothalamic neuropeptides will be activated or inhibited in order to modulate energy intake and expenditure and hence to maintain energy homeostasis. Notably, avian and mammalian species share many common signaling neuropeptides, such as NPY/AgRP, POMC/CART, ghrelin, and CCK (Richards, 2003). However these peptides do not always exhibit similar functions.

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A novel concept has recently emerged suggesting that kinase signaling pathways (mTOR and AMPK) from neuronal subpopulations in the hypothalamus might be involved in integrating signals from hormones such as ghrelin and insulin with fuel (nutrient) sensing mechanisms leading to adjustments in feed intake and energy expenditure (Richards and Proszkowiec-Weglarz, 2007). It has been found that ghrelin promotes feeding through modulation of hypothalamic mTOR pathway in rats (Martins et al., 2012). Until now, data on the role of the central mTOR signaling pathway in appetite regulation is non-existent in avian species. In contrast, several studies about AMPK signaling pathway in the chicken hypothalamus have been published recently (see below).

3. Role of (an)orexigenic peptides in mammals and avian species

The fact that birds and mammals utilize common signaling molecules does not necessarily mean that these compounds also share a common function (Table 1). We will briefly focus on orexins, ghrelin and growth hormone-releasing hormone (GHRH). Obestatin will be discussed in a separate section. Leptin remains controversial in avian species (Scanes, 2008) and this topic will not be discussed in this review.

Orexin-A and orexin-B are peptidergic neurotransmitters, and are alternatively known as hypocretin-1 and hypocretin-2, respectively, because they are found in the hypothalamus and are related to the incretin family of neurotransmitters (Katayama et al., 2010a). Orexin-A is a peptide consisting of 33 amino acid residues whereas orexin-B consists of 28 amino acid residues. Orexins (A and B) are potent orexigenic agents in mammals but are without any apparent effect on feed intake in chickens. Intracerebroventricular injection of mammalian orexins did not stimulate food intake in neonatal chicks (Furuse et al., 1999). However, Katayama et al. (2010b) found that intracerebroventricular injection of mammalian orexin-A stimulated monoamine metabolism in neonatal chicks. They also reported that intracerebroventricular injection of mammalian orexin-A, but not orexin-B, induced arousal of layer-type neonatal chicks (Katayama et al., 2010a). As mammalian orexin was used, conclusions about the effects of endogenous orex-

ins should be done cautiously. Chicken prepro-orexin cDNA has been cloned, sequenced and characterized. The predicted amino acid sequence of chicken prepro-orexin cDNA revealed that orexin-A and -B are highly conserved among vertebrate species (Ohkubo et al., 2002). However, no significant differences in orexin mRNA expression were observed in the hypothalamus of 24-h-fasted and ad libitum-fed chickens (Ohkubo et al., 2002). In contrast, orexin mRNA expression was significantly increased in the hypothalamus of 48-h-fasted broiler chickens (Song et al., 2012a), which revealed the possibility of orexin in the regulation of feed intake and/or energy balance under extreme conditions.

Ghrelin was originally identified as a growth hormone-releasing peptide and showed stimulatory effects on food intake in rodents and humans. Avian ghrelin has been cloned from chicken proventriculus and confirmed to be a 26-amino acid peptide, which shares 54% amino acid sequence identity with rat and human ghrelin. Interestingly, ghrelin exhibited inhibitory effects on feed intake when administered centrally to chickens (Saito et al., 2002). For more detailed information about the roles of ghrelin in regulating food intake and energy balance in avian species, the reader is referred to Kaiya et al. (2009).

GHRH participates in the control of feeding. However its effects might depend on the dosage used. For example, intracerebroventricular administration of picomole doses of GHRH stimulates food intake but nanomole doses of GHRH inhibited feeding in young Wistar male rats (Veyrat-Durebex et al., 2001). The intracerebroventricular injection of GHRP-2 (KP-102), a synthetic growth hormone secretagogue inhibited feed intake of neonatal chicks (Saito et al., 2002). Actually, ghrelin was originally identified as a growth hormone-releasing peptide. The different effects of ghrelin and GHRH on feed intake distinctly indicate that divergence exists in the action mode of growth hormone axis on energy homeostasis between mammalian and avian species.

4. Effect of feed restriction on hypothalamic neuropeptide gene expression

The effect of feed restriction on altering hypothalamic neuropeptide gene expression is hypothesized to represent a physiologically important adaptation in body weight homeostasis. Food restriction caused a significant increase of the prepro-orexin and NPY gene expression in obese mice in comparison with ad libitum fed animals (Yamamoto et al., 2000). Fasting stimulated hypothalamic NPY and AgRP mRNA and inhibited hypothalamic POMC mRNA in rats (Mizuno et al., 1999). Hypothalamic neuropeptide Y mRNA is increased after feed restriction in growing broilers (Boswell et al., 1999). In order to identify genes and gene networks differentially expressed in response to fasting and feeding of newly hatched chicks, a microarray analysis was conducted to evaluate global gene expression in the hypothalamus, which revealed that six genes were associated within a gene network (Higgins et al., 2010). Among these genes, the POMC gene was central to this network and its expression was significantly decreased with fasting (Higgins et al., 2010). In our recent work with 7- to 9-day-old chicks (Song et al., 2012a), mRNA levels of NPY, AgRP, melanocortin receptor 4 (MC4R), MCH and prepro-orexins were significantly upregulated in food-deprived chickens relative to their ad libitum fed counterparts. However, we observed that a food deprivation period of 48 h did not significantly alter hypothalamic POMC and CART mRNA levels, a finding which was different from the microarray study of Higgins et al. (2010). In contrast, a significant decrease in POMC mRNA levels in the hypothalamus of food-deprived broiler chicks was observed by Proszkowiec-Weglarz et al. (2006). Hen et al. (2006) also observed a significant down-regulation of POMC mRNA in hypothalami of 3-wk-old female

Table 1

Effect of (an)orexigenic peptides in avian species (icv, intracerebroventricular injection; iv, intravenous injection; ip, intraperitoneal injection; ↑, increase; ↓, decrease; ≈, unclear).^a

| Compound | Administration site | Response in feed intake in avian species |
|------------------------|---------------------|--|
| Ghrelin | icv, iv | ↓ (mammals ↑) ^b |
| Obestatin | iv, ip | No (mammals ≈) |
| α-MSH | icv | ↓ |
| CRF | icv | ↓ |
| Urocortin | icv | ↓ |
| NPY | icv | ↑ |
| AgRP | icv | ↑ |
| GHRH | icv | ↓ (mammals ↑) |
| MC3/4R agonists | iv, icv | ↓ |
| CART | icv | ↓ |
| μ-opioid agonists | icv | ↑ |
| Bombesin | icv | ↓ |
| Leptin ? | icv, iv | ↓ |
| Insulin | icv | ↓ |
| Peptide YY | icv | ↑ |
| Pancreatic polypeptide | icv | ↑ |
| Orexins-A/B | icv | ≈ (mammals ↑) |
| GLP-1 | icv | ↓ |

^a Based partly on data reported by, Denbow (1985), Richards (2003), Morton et al. (2006), Richards and Proszkowiec-Weglarz (2007).

^b Effect on mammals.

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