General and Comparative Endocrinology 190 (2013) 170–175

Contents lists available at SciVerse ScienceDirect

General and Comparative Endocrinology

journal homepage: www.elsevier.com/locate/ygcen

Update on ghrelin biology in birds

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ARTICLE INFO

Article history:
Available online 28 April 2013

Keywords:
Ghrelin
Des-acyl ghrelin
Ghrelin receptor
GOAT
Chicken
Quail

ABSTRACT

Ghrelin is a peptide found in the mucosal layer of the rat stomach that exhibits growth hormone–releasing and appetite-stimulating activities. Since the discovery of ghrelin in chicken in 2002, information on its structure, distribution, function, and receptors has been accumulated, mainly in poultry. Here, we summarize the following findings since 2008 in birds: (1) central ghrelin acts as an anorexigenic neuropeptide, but the effect of peripheral ghrelin differs depending on the chicken strain and light conditions the birds are kept in; (2) central ghrelin inhibits not only food intake but also water drinking, and it may be mediated by urocortin, a member of the corticotropin-releasing factor family; (3) peripheral ghrelin acts as an anti-lipogenic factor in broiler chickens but not in rats; (4) the enzyme involved in ghrelin acylation (ghrelin-*O*-acyltransferase [GOAT]) has been identified in chickens; (5) dietary lipids are used for ghrelin acylation; (6) des-acyl ghrelin administered alone or with ghrelin does not affect feeding behavior; (7) the existence and physiological function of obestatin must now be carefully examined in birds; (8) other than the growth hormone secretagogue receptors (GHS) R1a and 1b, GHS-R variants not found in mammals have been found in chicken and Japanese quail; and finally (9) little is known about the involvement of the ghrelin system in wild birds and in avian-specific behavior such as brooding and migration.

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1. Introduction

More than a decade has passed since ghrelin was discovered in 1999 (Kojima et al., 1999). Ghrelin was identified in rat stomach and in rats is a peptide that has growth hormone–releasing and appetite-stimulating activities (Kojima et al., 1999; Wren et al., 2000). Ghrelin has attracted attention because it is the only peptide hormone released from this peripheral organ that is known to stimulate food intake (Date et al., 2002). Ghrelin exists in various vertebrate species, including birds (Kaiya et al., 2002), and is involved in various physiological actions such as the regulation of pituitary hormones and feeding (Kaiya et al., 2008, 2011). Recently, progress has been made in the study of ghrelin, mainly in chicken and Japanese quail.

At the International Symposium on Avian Endocrinology in 2008, we proposed the following nine questions for the future study of ghrelin in birds that highlighted information that then was unknown (Kaiya et al., 2009): (1) Is endogenous ghrelin an anorexigenic hormone in birds? (2) Which sites within the brain are specifically targeted by ghrelin in birds? (3) What are the responses to peripherally administered exogenous ghrelin? (4) What are the enzymes involved in post-transcriptional acylation? (5) Which fatty acids are used to modify ghrelin, and how do they affect the function of ghrelin in birds? (6) What are the functions of des-acyl ghrelin in birds? (7) Is obestatin produced from preproghrelin and what role, if any, does it have in birds? (8) What are the roles of the ghrelin receptor identified in birds? and (9) How does ghrelin function in wild birds that exhibit behavior retained in domesticated poultry?

In the years since we posed these questions, reports have been published addressing the first eight questions, and here we summarize the relevant findings. The final question regarding the function of ghrelin in wild birds remains unanswered.

2. Is endogenous ghrelin an anorexigenic hormone in birds?

Ghrelin is a known orexigenic factor when administered peripherally or via the cerebral ventricle in rats (Tschöp et al., 2000; Wren et al., 2000). Plasma ghrelin levels increase when food is deprived and decrease after feeding (Toshinai et al., 2001), indicating that ghrelin is an endogenous, acute orexigen in rats (Fig. 1A).

In neonatal chickens, however, Furuse et al. (2001) reports that food intake is inhibited when ghrelin is administered via the cerebral ventricle. This anorexigenic effect is interesting because it is opposite to the orexigenic effect that is seen in rats (Fig. 2). The inhibitory effect of ghrelin on food intake has also been reported

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http://dx.doi.org/10.1016/j.ygcen.2013.04.014

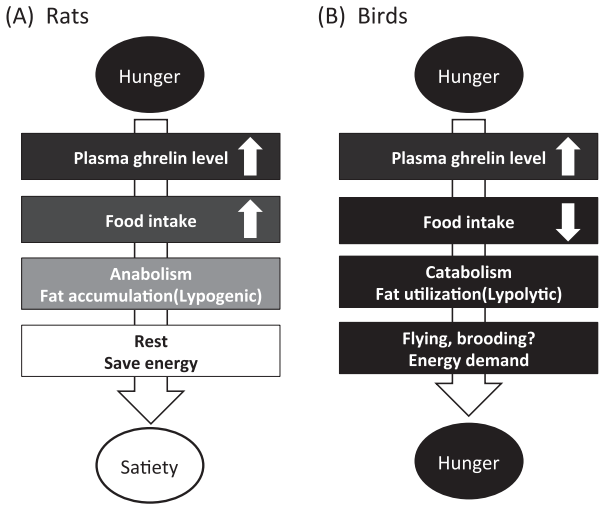


Fig. 1. Differences in the action of endogenous ghrelin between (A) rats and (B) birds. The figure illustrates how hunger signals influence ghrelin response and later actions. The density of the shadow shows the degree of hunger becoming lighter with increased satiety.

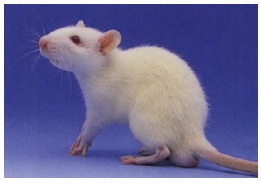
in Japanese quail (Shousha et al., 2005); therefore, the avian-specific mechanism of ghrelin action is of particular interest. Saito et al. (2005) focused on the hypothalamic–pituitary–adrenal axis, basing their research on evidence showing that in neonatal chickens peripheral administration of ghrelin increases plasma corticosterone levels (Kaiya et al., 2002) (Fig. 2) and that intracerebroventricular (ICV) administration of ghrelin increases vocalization, which is an anxiety behavior (Saito et al., 2002). They hypothesized the involvement of the corticotropin-releasing factor (CRF) system, and a study using a CRF receptor antagonist demonstrated that the CRF system, not the orexigenic NPY–orexin system shown in mammals, mediates the inhibitory effect of ghrelin on feeding (Saito et al., 2005). In accordance with the discovery of the involvement of the CRF system, Carvajal et al. (2009) demonstrated that ICV-administered ghrelin increases anxiety and memory retention via the CRF system.

It is likely that the inhibitory effect of ghrelin on feeding depends on the specific traits of the chicken strain evaluated. Xu et al. (2011) investigated the time course of the inhibitory effect of ICV-administered ghrelin in chicken lines of high or low body-weight and revealed that the threshold for the anorexigenic effect is lower in low body-weight chicks than in high body-weight chicks. In addition, ICV-administered ghrelin inhibited the AMP-activated protein kinase (AMPK) system in the hypothalamus. Xu et al. (2011) therefore hypothesized that the anorexigenic effect of ghrelin may be associated with hypothalamic AMPK signaling. These results indicate that endogenous ghrelin, or at least central ghrelin, acts as an anorexigenic neuropeptide in birds.

How plasma ghrelin levels change in broiler chickens when deprived of food is still unknown; however, in layer chickens, both plasma ghrelin level and ghrelin gene expression in the proventriculus are increased after 12-h fasting and have returned to the fed level 6 h after re-feeding (Kaiya et al., 2007). Similar results have also been reported in Japanese quail: plasma ghrelin level increased after 24-h fasting, and the elevated plasma level decreased 3 h after re-feeding (Shousha et al., 2005). These findings suggests that ghrelin acts as an endogenous "hunger signal" in both chickens and quail. However, the effect of peripheral administration of ghrelin in chickens is inconsistent with this concept because it inhibits food intake (Fig. 1).

It has been found that there are differences between chicken strains regarding the effect of ghrelin on feeding. With the same dose of peripherally administered ghrelin, no effect on food intake was seen in layer chicks (Kaiya et al., 2007); however, food intake was inhibited from 30 to 120 min after administration in broiler chicks (Geelissen et al., 2006). The inhibitory effect of peripheral ghrelin on food intake in broiler chicks was confirmed by two other independent studies (Buyse et al., 2009; Ocłoń and Pietras, 2011). Ocłoń and Pietras (2011) further investigated the mechanism of ghrelin-induced appetite suppression by using a glucocorticoid receptor antagonist, RU486, and a CRF type-2 receptor antagonist, astressin, in broiler chicks and demonstrated both the involvement of the hypothalamic–pituitary–adrenal axis as well as the inhibitory mechanism of central ghrelin (Fig. 2). It is still unclear whether ghrelin directly affects the brain or whether the vagal

Comparison of ghrelin's effects between rats and chickens



Effect	Comparison	Effect
Stimulation	**GH release**	Stimulation
No effect	**CORT release**	Stimulation
Stimulation	**Feeding (ICV)**	Inhibition
Stimulation	**Feeding (IV or IP)**	Stimulation/No effect/Inhibition
Increased	**Plasma ghrelin levels in fasted condition**	Increased
Lipogenic	**Lipid metabolism**	Lipolytic
Glucide	**Energy source**	Lipid
Contraction	**Gastrointestinal motility**	Contraction

Fig. 2. Comparison of the effects of ghrelin in rat and chicken. The effects of ghrelin on growth hormone (GH) release, corticosterone (CORT) release, feeding after intracerebroventricular (ICV) injection, feeding after intravenous (IV) or intraperitoneal (IP) injection, lipid metabolism, energy source, and gastrointestinal motility, and also plasma ghrelin levels in the fasted condition. Red letter indicates the effect that is different from rats.

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