

Conserved distal promoter of the agouti signaling protein (*ASIP*) gene controls sexual dichromatism in chickens

Eri Oribe, Ayaka Fukao, Chihiro Yoshihara, Misa Mendori, Karen G. Rosal, Sumio Takahashi, Sakae Takeuchi*

Graduate School of Natural Science and Technology, Okayama University, 3-1-1 Tsushima-naka, Kitaku Okayama 700-8530, Japan

ARTICLE INFO

Article history:

Received 18 January 2012

Revised 13 April 2012

Accepted 15 April 2012

Available online 23 April 2012

Keywords:

ASIP

Melanocortin

Feather

Pigmentation

Chicken

ABSTRACT

Brilliant plumage is typical of male birds, thus sexual plumage dichromatism is seen in many avian species; however, the molecular mechanism underlying this remains unclear. The agouti signaling protein (*ASIP*) is a paracrine factor that stimulates yellow/red pigment (pheomelanin) synthesis and inhibits black/brown pigment (eumelanin) synthesis in follicular melanocytes. In mammals, the distal promoter of the *ASIP* gene acts exclusively on the ventral side of the body to create a countershading pigmentation pattern by stimulating pheomelanin synthesis in the ventrum. Here, we examined the role of the distal *ASIP* promoter in controlling estrogen-dependent sexual dichromatism in chickens. Reverse-transcription polymerase chain reaction analyses revealed that *ASIP* class 1 mRNAs transcribed by the distal promoter were expressed exclusively on the ventral side of chicks and adult females displaying countershading. In showy adult males, the *ASIP* class 1 mRNAs were expressed in gold-colored ornamental feathers grown on the back. In the presence of estrogen, males molted into female-like plumage and *ASIP* class 1 mRNAs expression was altered to female patterns. These results suggest that the distal *ASIP* promoter produces countershading in chicks and adult females, similar to the ventral-specific *ASIP* promoter in mammals. In addition, the class 1 promoter plays an important role for creating sexual plumage dichromatism controlled by estrogen. This is the first evidence for a pigmentation gene having been modified in its expression during evolution to develop phenotypic diversity between individuals of different sexes.

© 2012 Elsevier Inc. All rights reserved.

1. Introduction

Coloration and color patterns exhibit tremendous diversity among animals of different or even the same species. This indicates that color of the body is ecologically important trait that is exposed to various selective pressures of natural selection including sexual selection [5]. In birds and mammals, a melanin-based pigmentation system is assumed to have been modified during individual species evolution for use in survival strategies, such as crypsis, aposematism, and sexual display. In fact, genetic analysis of coat or plumage color variation in natural environments has repeatedly identified variants of melanocortin 1 receptor (*MC1R*) and agouti signaling protein (*ASIP*) genes as sources of phenotypic diversity [1,11,14,17,18,20,21,26,28]. These genes are involved in regulating melanin-type switching.

The coloration of hairs in mammals is mainly determined by the distribution of two types of melanin, eumelanin and pheomelanin, which produce brown to black and yellow to red colorations, respectively. In birds, feather coloration can be formed by chemical (pigmentary) color, physical (structural) color, or a combination of

both. There are three major pigments used in feather coloration: melanins, carotenoids, and porphyrins [33]. Among the different types of colors, eumelanin and pheomelanin are the major pigments responsible for feather coloration in chickens. Both of these melanin-types are synthesized by melanocytes located in hair and feather follicle proximal regions. Melanocytes transfer melanins to epidermal cells that differentiate to components of the corresponding cutaneous appendages. The melanin-type synthesized in melanocytes is regulated by *MC1R*, a G protein-coupled receptor that activates the cAMP signaling pathway. Activity of *MC1R* stimulates the production of eumelanin, whereas inhibition of the receptor activity leads to the production of pheomelanin [2]. The activity of *MC1R* is augmented by melanocortin peptides, such as α -melanocyte-stimulating hormone (α -MSH) and adrenocorticotropic hormone (ACTH), whereas pheomelanin synthesis requires the binding of *ASIP* to *MC1R* [9,10,12,23].

In principle, an infinite number of pigment patterns can be created by changing the type of melanin produced by melanocytes depending on the region of the body; however, most mammals in nature display a common pigment pattern called countershading, a form of crypsis in which the dorsal side of the body is more darkly pigmented than the ventral side. In wild-type mice, the dorsal-ventral difference in pigmentation, light-bellied agouti

* Corresponding author. Fax: +81 86 251 7876.

E-mail address: stakeuch@cc.okayama-u.ac.jp (S. Takeuchi).

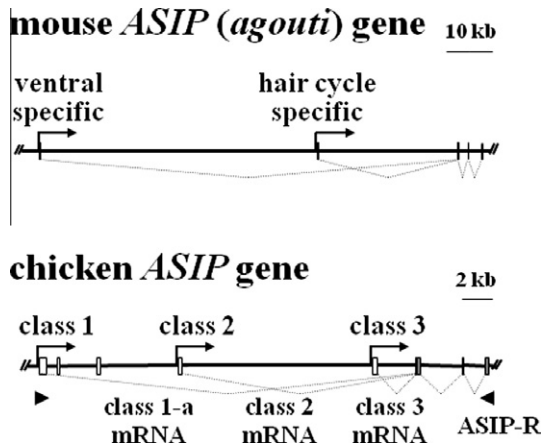


Fig. 1. Schematic representation of the mouse and chicken *ASIP* genes and their mRNA structure. Only major transcripts of each class of mRNA are shown. Exons are denoted by boxes and coding regions are indicated by shading. Arrows indicate the initiation site and direction of transcription. Arrowheads indicate the location of primers used in 5' RACE and/or RT-PCR.

pattern, is generated by the action of two different promoters of the *ASIP* gene, the proximal hair cycle-specific promoter and the distal ventral-specific promoter (Fig. 1) [3,19]. The hair cycle-specific promoter acts in hair follicles during the mid-portion of hair growth to produce black hair with a subapical yellow band [19,29], which creates the overall appearance of a mottled brown hair coat that provides adaptive coloration in the natural environment. The ventral-specific promoter, on the other hand, acts in hair

follicles throughout the hair cycle but only on the ventral side of the body, to produce entirely yellow or cream-colored ventral hairs [29]. Similarly, two promoters of the *ASIP* gene produce a light-bellied agouti pattern in rabbits [6]. Thus, our understanding about the molecular mechanisms for mammalian color pattern formation has advanced remarkably.

In chickens, chicks are covered with downy feathers (natal down feathers) at hatching and the pigment pattern of natal plumage is countershading (Fig. 2A). Plumage changes successively from natal plumage to juvenile and adult plumages by molting during the growth of chickens. Like the natal plumage, juvenile and adult female plumages are countershading with dull-colored feathers (Fig. 2B and D). In contrast, adult males are colorful with bright ornamental feathers on the back (Fig. 2C). Extensive studies have demonstrated that cryptic female plumage develops in the presence of estrogen, while the colorful plumage of males is in the default condition that results from the absence of gonadal hormones [13,24]; however, it remains unclear how estrogen signaling is related to the melanocortin system regulating melanin-type switching.

We previously demonstrated that the chicken *Extended black* locus controlling feather pigmentation encodes the *MC1R* and the dominant allele conferring black pigmentation encodes the constitutively active *MC1R* [16,27]. We also demonstrated that the wild-type *MC1R* binds α -MSH and ACTH, and activates adenylate cyclase [15]. *MC1R* gene mutations are also responsible for the various pigmentation phenotypes in wild birds [20,28]. Furthermore, we recently demonstrated that three classes of *ASIP* mRNA variants, class 1–3, are expressed by the action of three different promoters (Fig. 1) in feather follicles in which α -MSH and ACTH are produced [31,32]. Immunohistochemistry detected *ASIP* in

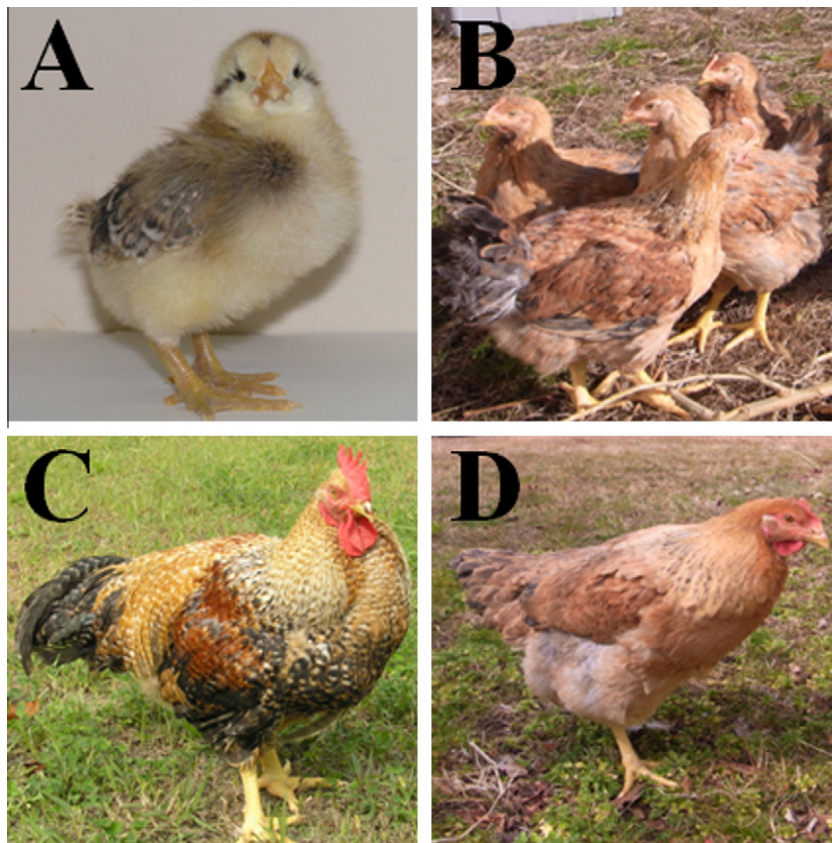


Fig. 2. Ontogenetic changes in plumage of Okayama-Jidori chickens. Photos of a one-week-old chick with natal plumage (A), juvenile female chickens (B), and adult male (C) and female (D) chickens.

Download English Version:

<https://daneshyari.com/en/article/2800538>

Download Persian Version:

<https://daneshyari.com/article/2800538>

[Daneshyari.com](https://daneshyari.com)