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Feeding responses to central administration of several somatostatin analogs in chicks

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ABSTRACT

Somatostatin is well known as an inhibitor of growth hormone release from the anterior pituitary. Its effects are exerted via 5 subtypes of receptors, which are named SSTR1 through 5. We recently reported that intracerebroventricular (ICV) injection of somatostatin stimulates feeding behavior in chicks. However, the specific receptors which mediate this orexigenic effect have not been identified in chicks. Thus, the purpose of the present study was to identify the receptor subtypes involved in somatostatin-induced feeding using 5 somatostatin analogs. Chicks that received vapreotide and octreotide (less than 3 nmol), which are agonist of SSTR2 and SSTR5, increased their food intake. Additionally, chicks ICV injected with BIM23056 or L-817,818 (SSTR3 and SSTR5 agonists, respectively) also had increased food intake. However, ICV injection of the SSTR4 agonist L-803,087 did not cause an orexigenic effect, suggesting that SSTR4 might not be important in somatostatin-induced feeding behavior. In summary, results from this study may be interpreted as SSTR2, SSTR3 and SSTR5 are related to somatostatin-associated feeding behavior in chicks.

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1. Introduction

Somatostatin is well known as a hypothalamic inhibitor of growth hormone (GH) release from the anterior pituitary (Brazeau et al., 1973; Ling et al., 1973). It is widely distributed in several tissues including the brain, gastrointestinal tract and pancreas (Polak et al., 1975; Brownstein et al., 1975; Alpert et al., 1976). Somatostatin binds to 5 subtypes of receptors, SSTR1 through 5 (Moller et al., 2003). These receptor subtypes are distributed in various tissues such as the anterior pituitary, spleen and brain (Bruno et al., 1993; Patel et al., 1995; Barnett, 2003).

In addition to the inhibitory effect on GH secretion, central somatostatin affects feeding behavior in mammals. For example, Vijayan and McCann (1977) demonstrated that intracerebroventricular (ICV) injection of somatostatin suppressed feeding behavior of rats. Aponte et al. (1984) reported that centrally administered somatostatin caused a biphasic effect: it decreased feeding behavior of fed rats while stimulated feeding behavior in fasted rats. Additionally, Feifel and Vaccarino (1990) found that central administration of somatostatin at low doses (pmol order) stimulated feeding behavior while higher doses (nmol order) decreased it. Thus the effect of somatostatin on feeding behavior seems to be dependent on several factors. In rats, ICV injection of octreotide, a SSTR2 and SSTR5 agonist, stimulated feeding behavior (Beranek et al., 1999). It is therefore likely that these receptors are related to somatostatin-related feeding behavior in rats.

The amino acid sequences of chicken and mammalian somatostatin are identical (Hasegawa et al., 1984). In chickens, somatostatin is distributed in the brain (Shiosaka et al., 1981; Takatsuki et al., 1981) and peripheral tissues such as pancreas (Weir et al., 1976) and gastrointestinal tract (Rawdon and Andrew, 1981) as is the case in mammals. Somatostatin also has an inhibitory effect on GH release in chickens (Harvey and Scanes, 1987; Scanes and Harvey, 1989). As in mammals, somatostatin affects food intake of chicks (Tachibana et al., 2009), but unlike in mammals, ICV injection of somatostatin consistently stimulates feeding behavior in chicks irrespective to feeding condition or dose. Cortistatin, which has structural similarity to somatostatin and binds to somatostatin receptors (De Lecea et al., 1996; Fabre et al., 2004), also stimulates feeding behavior of chicks when administered centrally (Tachibana et al., 2009). As in mammals, the nucleotide sequences of the 5 chicken somatostatin receptors have been determined (Li et al., EMBL database). These receptors are similar to mammals; for example, the homologies of chicken SSTR1, SSTR2, SSTR3 SSTR4 and SSTR5 to rat counterparts are 81, 86, 64, 66 and 69%, respectively (GenBank accession nos. EU283412.1, AY954511.1, DQ003337.1, DQ069274.1 and AY954512.1). However, the specific receptors which are involved in somatostatin-induced feeding behavior in chicks have not been clarified.

The purpose of the present study was to determine the contribution of somatostatin receptors to somatostatin's orexigenic effect in chicks. We used various somatostatin receptor agonists including vapreotide, octreotide (both SSTR2 and SSTR5 agonists), BIM23056 (SSTR3 agonist), L-803,087 (SSTR4 agonist), and L-817,818 (SSTR5 agonist, Hannon et al., 2004) and measured food intake to elucidate which receptor type mediated somatostatin's orexigenic effect.

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2. Materials and methods

2.1. Animals

Day-old male layer chicks (*Gallus gallus*, White Leghorn, Julia, Ninobe Hatchery, Kagawa, Japan) were raised in a room kept at 30 °C with continuous lighting. A commercial diet (crude protein: 24%, metabolizable energy: 3050 kcal/kg, Toyohashi Feed Mills Co. Ltd, Aichi, Japan) and water were available *ad libitum*. Before each experiment, body weights were measured and chicks were distributed into groups so that the average body weight was as uniform as possible between treatment groups. The chicks were maintained in accordance with the recommendations of the National Research Council (National Research Council, 1996), Guide for Care and Use of Laboratory Animals and the Guidance for Experiments in Ehime University and the Law (No.105) and Notification (No.6) of the Japanese Government.

2.2. Drugs, ICV injection and measurement of food intake

Somatostatin (Peptide Institute, Osaka, Japan), vapreotide (agonist of SSTR2 and SSTR5, American Peptide Company, CA, USA), octreotide (agonist of SSTR2 and SSTR5, Bachem AG, Bubendorf, Switzerland), BIM23056 (agonist of SSTR3), L-803,087 (agonist of SSTR4), and L-817,818 (agonist of SSTR5, Tocris Bioscience, Bristol, UK) were dissolved in a saline solution that contained 0.1% Evans Blue dye. This saline solution was used as a vehicle and as the control treatment. For L-803,087 and L-817,818, 5% dimethyl sulfoxide (DMSO) was added to facilitate their dissolution and the saline solution containing DMSO was used for the control treatment. ICV injections were performed according to a method reported previously (Davis et al., 1979). Briefly, the head of the chick was inserted into an acrylic box which had a hole at the top plate. The injection coordinates were 3 mm anterior to the coronal suture, 1 mm lateral from the sagittal suture, and 3 mm deep targeting the left lateral ventricle. Anatomical landmarks were determined visually and by palpation. The peptide solution was injected through the hole, using a microsyringe, at a volume of 10 μL. This method is not stressful for chicks since the ICV injection of saline solution, which was used as the control, did not affect feeding behavior (Furuse et al., 1999) or corticosterone release (Saito et al., 2005) when compared with intact chicks without injections. All injections were made between 8:00 and 10:00 under an ad libitum feeding condition.

At the end of each experiment, the chicks were sacrificed with an overdose of pentobarbital. The brain was then removed to confirm the accuracy of injection. Any chicks that did not have Evans Blue dye in the lateral ventricle were not used for further analyses. We used 11 chicks in each group for ICV studies. The number of chicks which was available for data analysis is described in the figure legends.

2.3. Experiment 1: effect of somatostatin on feeding behavior

Six-day-old chicks were ICV injected with 0 (vehicle only), 0.3 or 3 nmol somatostatin. These doses were decided based on our previous study (Tachibana et al., 2009). A pre-weighed food container was then given to each chick. Food intake was measured at the accuracy of 0.001 g at 30 and 60 min post injection.

2.4. Experiment 2: effect of SSTR2 and SSTR5 agonists on feeding behavior

Vapreotide was used to investigate the involvement of SSTR2 and SSTR5 on somatostatin-induced feeding. Six-day-old chicks were ICV injected with 0 (vehicle only), 0.3 or 3 nmol vapreotide and then their food intake was measured at 30 and 60 min post injection.

Octreotide was also used to investigate the involvement of SSTR2 and SSTR5 on somatostatin-induced feeding. Five-day-old chicks were ICV injected with 0 (vehicle only), 0.3 or 3 nmol octreotide and food intake was measured at 30 and 60 min post injection.

2.5. Experiment 3: effect of SSTR3 agonist on feeding behavior

BIM23056 was used to investigate the effect of SSTR3. Six-day-old chicks were ICV injected with 0 (vehicle only), 0.3 or 3 nmol BIM23056 and food intake was measured at 30 and 60 min post injection.

2.6. Experiment 4: effect of SSTR4 agonist on feeding behavior

L-803,087 was used to investigate the effect of SST4R. Six-day-old chicks were ICV injected with 0 (vehicle only), 0.3 or 3 nmol L-803,087 and food intake was measured at 30 and 60 min post injection.

2.7. Experiment 5: effect of SSTR5 agonists on feeding behavior

L-817,818 was used to investigate the effect of SSTR5. Seven-day-old chicks were ICV injected with 0 (vehicle only), 0.3 or 3 nmol L-803,087 and food intake was measured at 30 and 60 min post injection.

2.8. Experiment 6: effect of higher dose of SSTR4 and SSTR5 agonists on feeding behavior

Seven-day-old chicks were ICV injected with 0 (vehicle only), 15 nmol L-803,087 or 15 nmol L-817,818 and food intake was measured at 30 and 60 min post injection.

2.9. Statistical analysis

Data were statistically analyzed with two-way repeated analysis of variance (ANOVA). The Tukey–Kramer test was used at each time point as a post hoc test. Significant difference was set at $P<0.05$. Data are expressed as mean ± SEM.

3. Results

3.1. Experiment 1: effect of somatostatin on feeding behavior

Fig. 1 shows that ICV injection of somatostatin significantly increased food intake [$F(2,20)=21.88$, $P<0.05$]. In the ad libitum feeding study, 3 nmol somatostatin significantly increased food intake at all times. The

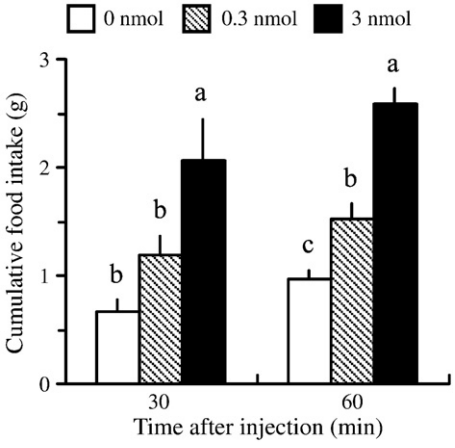

Fig. 1. Effect of ICV injection of somatostatin on feeding behavior in chicks. Data are expressed as means ± SEM. The number of chicks in the ad libitum study was as follows: 0 nmol, 7; 0.3 nmol, 9; 3 nmol, 7. Groups with different letters are significantly different at each time point ($P<0.05$).

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