

EFFECTS OF SEROTONIN ON THE FOOD INTAKE IN CHICKENS IN THE POST-HATCHING PERIOD

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Abstract

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The effect of serotonin (5-HT) on food intake in the post-hatching period was studied in 360 Hybro broilers from 1 to 25 days of age in 3 experimental series. They were reared in batteries and had free access to food and water. The experimental chickens (4 groups of 10 or 20 birds) were each intraperitoneally given single doses of 1 or 2 mg 5-HT (Sigma Corp., USA), four groups were sham-injected with saline, and four groups were left untreated. The food intake of experimental and control groups was measured 30 and 60 min post injection and then at 1-h intervals till 1400 h. Cumulative food intake for the interval 0700 to 1400 h and per 24 h was also recorded.

The 5-HT administration did not affect the food intake of chickens 1 and 2 days of age. On day 3, however, the birds began to respond to 5-HT administration in that its higher dose stopped eating in the first post-injection hour, the lower dose (1 mg · kg⁻¹) suppressed it significantly as compared to sham-injected ($P < 0.01$) and intact controls ($P < 0.02$). The food intake of experimental chickens at all other ages under study (i. e. on days 4, 5, 9, 11, 17 and 25) was similarly suppressed in the first post-injection hour compared to either control groups. No dose-dependent effect of 5-HT was detected. In older birds, consuming increasingly larger portions in the first morning hour, the 5-HT induced abstinence was also manifested in cumulative food intake from 0700 to 1400 h. Their actual food consumption was lower at 17 ($P < 0.01$) and 25 ($P < 0.01$) days of age, the relative food intake at 17 ($P < 0.01$) days. Expressed in terms of 24-h consumption the 5-HT inhibited eating during the first morning hour became apparent especially in 25-d-old birds ($P < 0.05$). It is noteworthy that no differences in food consumption of sham-injected and intact controls were found.

The fact that the ingestive response to peripheral administration of 5-HT did not occur until day 3 suggests that maturation of some components of the serotonergic system in the fowl continues after hatching.

Age, broiler, intraperitoneal administration, 5-HT

In birds, serotonergic mechanisms are involved in the regulation of numerous physiological functions. Their morphological substrates and the presence of serotonin (5-HT) in various tissues have been demonstrated (Juorio and Vogt 1967; Epstein et al. 1980; Gershon et al. 1980; Cassone et al. 1983; Wallace 1985). In the blood plasma of cocks 3—7 mg · kg⁻¹ have been found (Freeman 1984).

A number of studies on 5-HT have shown that this neurotransmitter affects the cardiovascular and respiratory systems of pigeons and poultry, exerts an excitatory effect on the electromyographic activity of the esophagus of the adult pigeon, and is involved in energy metabolism and thermoregulation affecting their circadian rhythms in chickens (Cogburn et al. 1976; Freeman 1979; Hillman et al. 1980; Fileccia et al. 1987; Hohtola et al. 1989).

Serotonin administered centrally or peripherally also affects the behaviour of birds; in chickens

of various ages different doses of 5-HT have been reported to produce tonic immobility, lethargy, somnolence and sleep, but also increased activity (Hehman et al. 1961; Dewhurst and Marley 1965; Hanig and Seifter 1973; Hennig 1980; Hennig et al. 1988).

Serotonin has also been demonstrated to exert an effect on ingestive behaviour: its intracerebroventricular administration decreased food intake in broilers and turkeys fed ad libitum, but had no effect when given to birds previously starved (Denbow et al. 1982; Denbow 1984).

Effects similar to those of 5-HT have also been observed in birds treated with its precursor, tryptophan, systemic administration of which affects, e. g., the behaviour of chickens (Gallup et al. 1977). The concentration of 5-HT in the brain of adult turkeys doubled after feeding surplus tryptophan for several days (Lee and Britton 1982); intragastric administration of tryptophan decreased food consumption of older broilers and laying type chickens (Lacy et al. 1982). A commercial mixture of 20 amino acids (AA), containing tryptophan (Nutramin Neo 8 % Spofa, Czechoslovakia), administered intraperitoneally to broilers aged 2 to 27 days post-hatching, markedly suppressed their food intake for longer than 12 hours. However, this phenomenon first occurred in birds 5 days of age. In 3-d-old birds food intake was slightly suppressed only in the first post-injection hour and chickens 2 days of age showed no response (Baranyiová 1987ab).

To throw further light on the post-hatching development of the aminostatic food intake regulation, a component of which the serotonergic system, no doubt, is, the present experiments were designed to find at what age the food intake of chickens begins to respond to peripheral administration of 5-HT.

Materials and Methods

A total of 360 Hybro broilers were used in three experimental series (see Table 1). In view of "a significant tendency for the birds to feed as a group rather than as individual extended over the entire day" (Hughes 1971) we made the sizes of the groups similar to those under natural conditions to ensure undisturbed feeding behaviour of chickens.

The birds were reared in temperature controlled wire-floored battery brooders and allowed free access to food BR I (starter) and BR II (grower) and water. The relative humidity in the animal room was between 50 and 60 %.

The birds were weighed daily between 0600 and 0700 h during the maintenance. To measure their food intake, filled and preweighed feeders were installed at 0700, reweighed and refilled daily at 1400 and 1900 h. Food spillage was minimized. On days of 5-HT administration the food consumed was weighed 30 and 60 min post injection and then at hourly intervals till 1400 h.

The experimental birds were each intraperitoneally injected with a single dose of 1 or 2 mg .kg⁻¹ (Pollock and Rowland 1981) of 5-HT (5-hydroxytryptamine creatinine sulphate, Sigma) 2 to 3 min before 1900 h on day 1, and 2–3 min before 0700 on all other days specified in Table 1.

Table 1

Design of the experiment

Day	No. of groups (No. of birds in parentheses)			
	5-HT treated		Controls	
	dose mg . kg ⁻¹	Intact	NaCl treated	
Series 1	1	4(10) 2*	—	
	2	4(10) 2	4(20)	
	3	4(10) 2	4(20)	
	4	4(10) 2	4(20)	
Series 2	5	4(20) 2	4(20)	
	11		4(20)	
	17	4(10) 2	4(10)	
	25	4(10) 2	4(10)	
Series 3	1	4(10) 1	4(10)	
	2	4(10) 1	4(10)	
	3	4(10) 1	4(10)	
	4	4(10) 1	4(10)	
	5	4(10) 1	4(10)	
	9	2(10) 2	3(10) 1	2(10)
	11	4(10) 2		4(10)

* Pollock and Rowland (1981)

In view of the short-lasting action of 5-HT and its rapid inactivation by lung, liver, thrombocytes and blood plasma (Gershon and Tamir 1984) the times of injections were exactly recorded and the birds and the respective controls had immediately access to food. Their consumption was measured 30 min later (except days 1, 2, 3, 4 and 17 at the 2 mg . kg⁻¹ dose) and then as described above. Cumulative food intake for the interval 0700 to 1 400 h and per 24 h was also recorded, and actual and relative consumption calculated.

The control birds were either left untreated (series 1 and 2) (Baranyiová 1988b) or sham-injected with saline (series 3) in volumes corresponding to those of 5-HT solutions. The experimental and control groups were alternated.

Food intake of the individual groups was calculated per bird. The significance of the differences between mean values for the treated and control groups was assessed by Student's t-test.

Results

Administration of either 1 or 2 mg . kg⁻¹ of 5-HT had no effect on the food intake of 1 and 2-days-old chickens (Fig. 1 and 3). A slight difference between sham-injected and intact controls on the 2nd post-hatching day was not significant.

On day 3, however, the food intake of birds given 1 mg . kg⁻¹ 5-HT was markedly suppressed as against sham-injected controls ($P < 0.01$) thirty min and against intact controls ($P < 0.02$) sixty min post injection (Fig. 1 and 3). Birds treated with 2 mg . kg⁻¹ 5-HT did not initiate eating in the first post-injection hour but

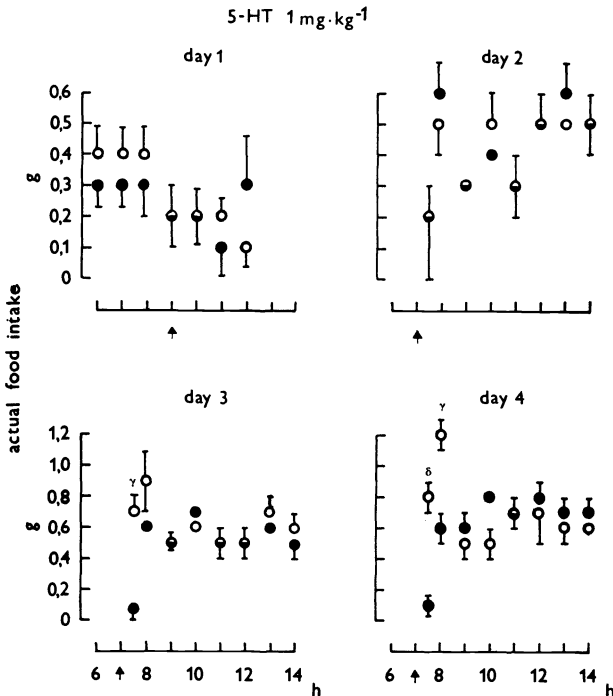


Fig. 1. Actual food intake of chickens aged 1 to 4 d ($g \pm$ S.E.M. per bird) treated with 1 g . kg⁻¹ 5-HT (●) and saline-treated controls (○); $\alpha = p < 0.05$, $\beta = p < 0.02$, $\gamma = p < 0.01$, $\delta = p < 0.001$. The arrows indicate the 5-HT injection.

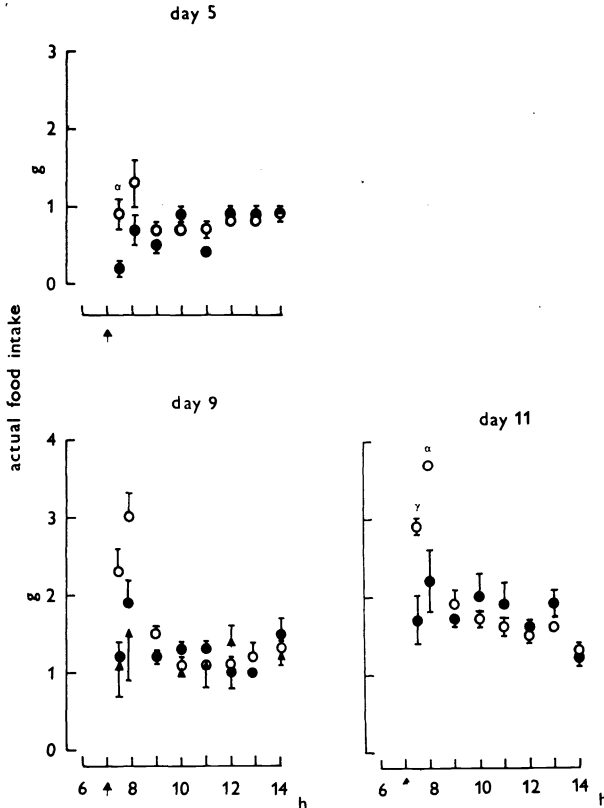


Fig. 2. Actual food intake of chickens aged 5 to 11 d (\pm S.E.M. per bird) treated with 1 mg \cdot kg⁻¹ 5-HT (\bullet) and saline-treated controls (\circ). On d 9, also 2 mg \cdot kg⁻¹ dose (\blacktriangle) was included.

compensated for the abstinence in the following two hours when they ate more than the intact controls ($P < 0.05$; $P < 0.01$). There was practically no difference between sham-injected and intact controls (0.9 ± 0.2 vs 1.0 ± 0.1 g).

A similar response to 5-HT administration was observed in chickens 4, 5, 9, 11, 17 and 25 days of age (Fig. 2 and 4). However, no dose-dependent effect on food intake was found. On days 2, 3, 4, 5 and 11 both intact and sham-injected controls were included: no differences in their food intake were found.

The food consumption by the end of the first morning hour of the experimental birds was substantially lower than that of controls. This was also manifested in their intake between 0700 and 1400 h particularly in birds aged 17 and 25 days (the actual food consumption) ($P < 0.01$; $P < 0.01$) and 17 days (the relative food consumption) ($P < 0.01$) as shown in Fig. 5. Also the 24-h food intake (Fig. 6) was lower in 5-HT-treated chickens ($P < 0.05$) 25 days of age as a result of the reduced food intake in the post-injection hour.

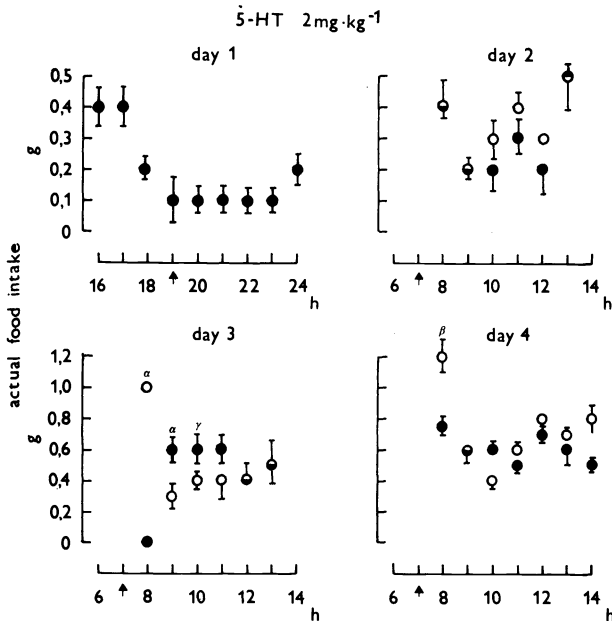


Fig. 3. Actual food intake of chickens aged 1 to 4 d ($g \pm$ S.E.M. per bird) treated with 2 mg . kg⁻¹ 5-HT (●) and intact controls (○).

Discussion

The food intake of adult fowl is suppressed when individual AA are either infused into the hepatic portal vein (lysine, leucine) of previously starved birds (Rusby and Forbes 1987) or administered intragastrically (tryptophan and tyrosine) (Lacy et al. 1982). On the other hand, an i. p. injection of 20 AA containing also tryptophan had no such effect in chickens on day 2 after hatching. However, it did begin to reduce their food intake on day 3; between 5 and 27 days of age this effect was profound and lasted more than 12 h (Baranyiová 1987ab).

The administration of 5-HT also failed to affect the food intake and ingestive behaviour of chickens on days 1 and 2 post hatching. In this case a possible interference with residual yolk absorption cannot be excluded. However, on day 3 either of the two doses of 5-HT suppressed markedly the food intake of treated birds. Their behaviour was also affected particularly with the higher 5-HT dose. They were mostly apathic, squatted and fell asleep with fluffed plumage. During the first 30 min after 5-HT administration the younger birds pecked at food very rarely. For example, 5-days-old chickens showed an average latency of 3 min from 5-HT injection to first food pecking: among 10 birds in the group only 3 pecked occasionally. This was reflected in food intake of only 0.2 ± 0.06 g . h⁻¹ per bird. Thus the 5-HT administration seemed to induce satiety the duration of which was dependent upon the action of 5-HT. In marked contrast, intact controls consumed food so voraciously, especially in the first morning hour (i. e. after the maintenance and refilling the feeders — the so-called caretaker effect described by Squibb and Collier, 1979), that this first meal represented

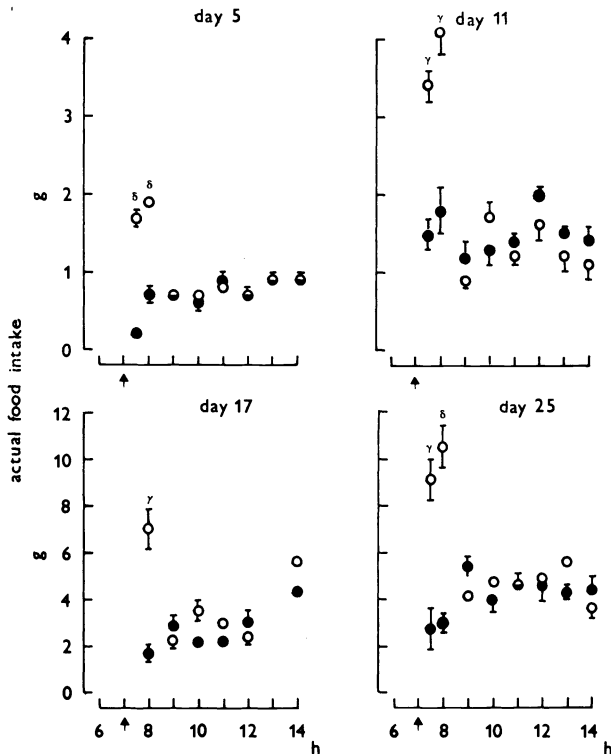


Fig. 4. Actual food intake of chickens aged 5 to 25 ($\text{g} \pm \text{S.E.M.}$ per bird) treated with $2 \text{ mg} \cdot \text{kg}^{-1}$ 5-HT (●) and intact controls (○).

in broilers up to 4 weeks of age as much as 15% of their daily consumption (Baranyiová 1988a). Similar consumption and behaviour was observed in our sham-injected controls.

Of all experimental series on days 2, 3, 4, 5, 9 and 11 intact and sham-injected controls were compared. No differences were found in food intake between these groups in keeping with our previous results (Baranyiová 1987a). From the present experiment it also appears that under our conditions provided the gentle handling treatment with saline did not interfere with food intake which implies that intact controls can be regarded as fully adequate in this type of study.

On the other hand, the dose-dependent effect of 5-HT as described by Leibowitz and Shor-Posner (1986) and others was very slight. An explanation of this may be the timing of 5-HT administration into the phase of most active eating period (Squibb and Collier 1979; Savory 1980; Baranyiová 1988a) when the drive to eat is strong and may well mask the subtle differences in response of the two 5-HT doses. Further work is needed to elucidate this question.

Since the blood-brain barrier of chickens is permeable to monoamines approximately till the end of the first post-hatching month (Callingham and Cass 1966; Hanig et al. 1970; Hanig and Seifter 1973), the suppressive effect of 5-HT on their food consumption may be central, peripheral or combined. Of interest in this connection is the finding that the central morphological components

7 to 14 h

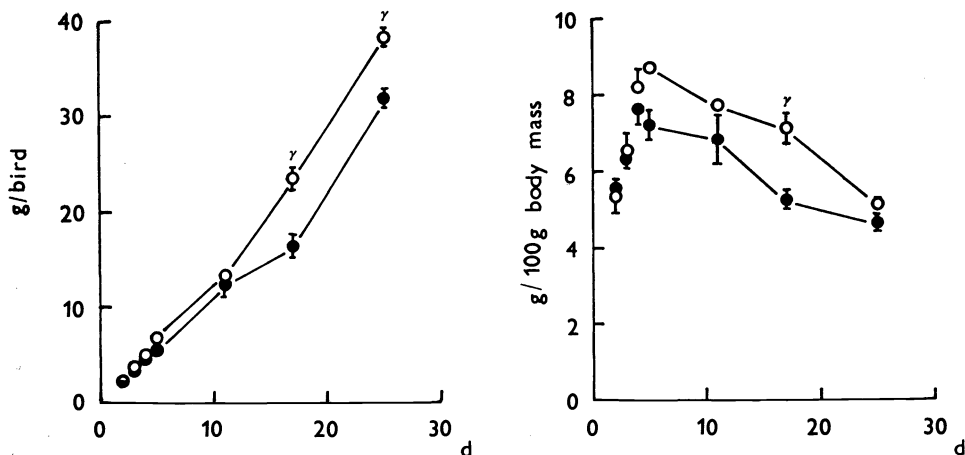


Fig. 5. Actual and relative food intake of chickens aged 1 to 25 d treated with $2 \text{ mg} \cdot \text{kg}^{-1}$ 5-HT (●) in the interval 0700 to 1400 h and of intact controls (○).

per 24 h

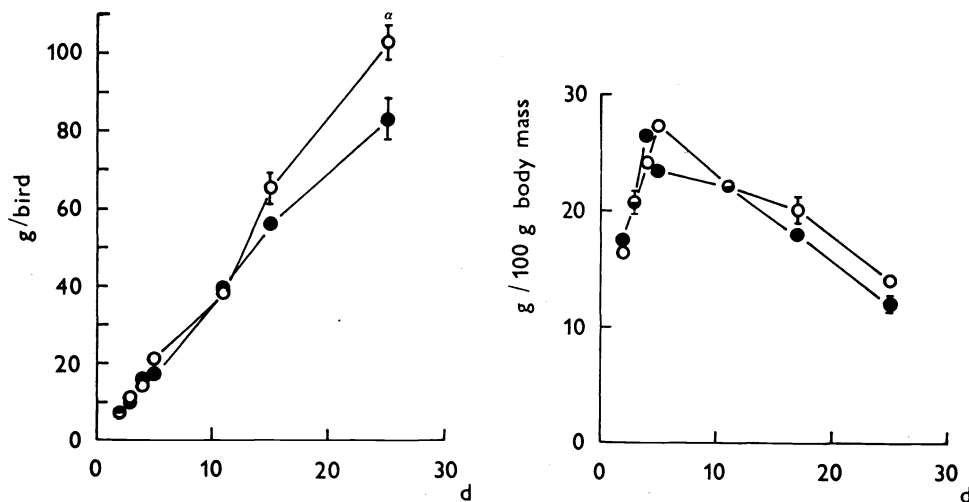


Fig. 6. Actual and relative food intake of chickens aged 1 to 25 d treated with $2 \text{ mg} \cdot \text{kg}^{-1}$ 5-HT (●) and intact controls (○) per 24 hours.

of the serotonergic system occur early in the embryonic development: serotonergic neurons appear from day 4 in the brainstem, from day 12 in the hypothalamus with the mature organization of the 5-HT cell groups occurring by day 17 (Wallace 1985). The regional distribution of 5-HT content in the chicken brain parallels its distribution in the rat (Cassone et al. 1983).

With peripheral administration of 5-HT its ubiquitous presence in the body,

especially in the digestive tract, should be considered; for example, in the intestine it is synthesized in ribosomes and stored in secretion granules of enterochromaffin cells (Nemoto et al. 1983). Here more than 90 % of 5-HT contained in the body are localized (Erspamer 1961 in Pilot et al. 1983).

In the fowl digestive tract, the 5-HT neurons first appear in the duodenal mucosa of embryos between day 5 and 7; between day 9 and 13 the number of autoradiographically detected axons increases (Epstein et al. 1980). Gershon et al. (1980) have shown that the 5-HT concentration before day 15 of incubation is very low in the intestinal wall of chicken embryos cleaned of its mucosa and it substantially increased between day 19 of incubation and the 4th post-hatching week. The authors proposed a hypothesis that precursors of enteric serotonergic neurons differentiate within the gut mesenchyme, then enter the myenteric plexus and gradually elaborate axons. Once the axon is formed, the 5-HT uptake mechanisms concentrate in its plasma membrane and a transmitter store develops. It has also been shown that changes in ^3H -5-HT uptake pattern in the gut are age-dependent, and that maturation of serotonergic elements depends on the developmental changes in the microenvironment of the gut (Epstein et al. 1980).

Age is, among other factors, considered to be a source of variability in 5-HT effects on temperature regulation in newly hatched chickens (Freeman 1979). This author found 5-HT to be an excitatory transmitter involved in heat loss mechanisms.

The fact that the nutritional response to peripheral administration of 5-HT did not occur until day 3, i. e. later than the thermoregulatory response, suggests that maturation of the components of the serotonergic system continues after hatching and the physiological effects of 5-HT begin to come into play at various ages and apparently also change with advancing age.

Vliv serotoninu na konzum potravy kuřat po vylíhnutí

Vliv serotoninu (5-HT) na příjem potravy byl sledován na 360 broilerech Hybro ve věku 1 až 25 dnů. Kuřata byla držena v bateriích a měla volný přístup ke krmivu a pitné vodě. Pokusným jedincům (vždy 4 skupiny po 10 či 20 kusech) byly jednorázově intraperitoneálně aplikovány dávky 1 ev. 2 mg · kg⁻¹ 5-HT (Sigma), 4 skupinám byl stejnou cestou podán fyziologický roztok a 4 skupiny byly intaktní. Konzum potravy pokusných a kontrolních skupin byl měřen 30 a 60 min po ošetření a poté v lhodinových intervalech do 14 h. Kumulativní příjem potravy jsme měřili v intervalu 7–14 h a za 24 h.

Podání 5-HT neovlivnilo příjem potravy u kuřat v 1. a 2. dnu po vylíhnutí. Třetí den však kuřata počala na podaný 5-HT odpovídat tím, že jeho vyšší dávka zastavila příjem potravy v 1 h po aplikaci, dávka nižší (1 mg · kg⁻¹) ho významně snížila ve srovnání s kontrolami ošetřenými fyziologickým roztokem ($P < 0.01$) i s kontrolami intaktními ($P < 0.02$). Příjem potravy pokusných kuřat ostatních věkových skupin (tj. 4., 5., 9., 11., 17. a 25. dne) byl podobně ovlivněn v 1 h po aplikaci 5-HT ve srovnání s oběma kontrolami. Závislost účinku 5-HT na dávce nebyla nalezena. U starších kuřat, konzumujících vzrůstající množství potravy v 1. ranní hodině, se abstinence serotoninem navozená projevila i v kumulativním konzumu mezi 7. a 14. h. Absolutní konzum potravy byl nižší u kuřat 17. ($P < 0.01$) a 25. dne ($P < 0.01$), relativní konzum 17. dne ($P < 0.01$). Konzum za 24 h byl ovlivněn zejména u kuřat 25denních ($P < 0.05$). Rozdíly mezi

kontrolami ošetřenými fyziologickým roztokem a kontrolami intaktními nebyly nalezeny.

Skutečnost, že nutriční odpověď na periferní podání 5-HT se objevila až 3. dne po vylíhnutí, naznačuje, že dozrávání komponent serotoninergního systému u kuřat pokračuje i po vylíhnutí.

Влияние серотонина на потребление пищи цыплят после вылупления

Исследование влияния серотонина (5-HT) на потребление пищи проводили на 360 бройлерах Гибро в возрасте 1 – 25 суток. Цыплят содержали в клеточных батареях со свободным доступом к кормушке и питьевой воде. Подопытным особям (всегда 4 группы по 10 или 20 цыплят) единовременно вводили интраперитонеально дозы 1 или 2 мг.кг⁻¹ 5-HT (Сигма), 4 группам одинаковым путем вводили физиологический раствор и 4 группы оставались без препаратов. Потребление пищи подопытных и контрольных групп измеряли через 30 и 60 минут после дачи препаратов и, впоследствии, в интервалах 1 час до 14 часов. Кумулятивный прием пищи измеряли в интервале 7 – 14 часов в течение 1 суток.

Дача 5-HT не оказывала влияние на потребление пищи у цыплят в возрасте 1 и 2 суток после вылупления. Однако на третий день на прием 5-HT следовал ответ, соответственно которому его более высокая доза вылилась в прекращение приема пищи 1 час после введения, более низкая доза (1 мг.кг⁻¹) существенно прием пищи понижала по сравнению с контрольными группами, которым вводили физиологический раствор ($P < 0,01$) и группами, не принимавшими никаких препаратов ($P < 0,02$). На прием пищи подопытных цыплят остальных возрастных групп (т. е. 4, 5, 9, 11, 17 и 25 суток) по сравнению с обеими контрольными группами оказывал аналогичное влияние 5-HT один час после его введения. Незначительная зависимость воздействия 5-HT от дозы не была существенной. У цыплят постарше, потребляющих увеличивающееся количество пищи в течение первого утреннего часа, вызванная серотонином разгрузка проявилась также в кумулятивном потреблении между 7 и 14 часами. Абсолютное потребление пищи было меньше у цыплят в возрасте 17 ($P < 0,01$) и 25 суток ($P < 0,01$), относительное потребление – 17 суток ($P < 0,01$). Разница между принимающими физиологический раствор контрольными группами и группами без препаратов не была установлена.

Обстоятельство, что нутритивный ответ на периферийную дачу 5-HT имел место только на 3 сутки после вылупления, свидетельствует о том, что созревание компонентов serotoninергической системы цыплят продолжается также после вылупливания.

References

- BARANYIOVÁ, E.: Effect of intraperitoneal administration of amino acids on the food intake of chickens in the first month after hatching. *Acta vet. Brno* **56**, 1987a: 417–426
- BARANYIOVÁ, E.: Effect of intraperitoneal administration of amino acids on food intake of chickens aged 1 to 12 days. *Physiol. bohemoslov.* **36**, 1987b: 520

- BARANYIOVÁ, E.: Zirkadiane Periodik der Futteraufnahme bei Broilern in den ersten 30 Tagen nach dem Schlupf. *Mh. Vet. Med.* **43**, 1988a: 863–865
- BARANYIOVÁ, E.: Effect of intraperitoneal administration of serotonin on food intake of chickens aged 1 to 25 days. *Physiol. bohemoslov.*, **37**, 1988a: 552
- CALLINGHAM, B. A.—CASS, R.: Catecholamines in the chick. In *Physiology of the Domestic Fowl* (ed. by HORTON-SMITH, C.—AMOROSO, E. C.), Oliver — Boyd, Edinburgh, 1966, pp. 279–285
- CASSONE, V. M.—LANE, R. F.—MENAKER, M.: Daily rhythms of serotonin metabolism in the medial hypothalamus of the chicken: effect of pinealectomy and exogenous melatonin. *Brain Res.* **289**, 1983: 129–134
- COGBURN, L. A.—HARRISON, P. C.—BROWN, D. E.: Scotophase-dependent thermoregulatory dysfunction in pinealectomized chickens. *Proc. Soc. exp. Biol. Med.* **153**, 1976: 197–201
- DENBOW, D. M.—Van KREY, H. P.—CHERRY, J. A.: Feeding and drinking response of young chicks to injections of serotonin into the lateral ventricle of the brain. *Poult. Sci.* **61**, 1982: 150–155
- DENBOW, D. M.: Body temperature and food intake of turkeys following ICV injections of serotonin. *Nutr. Behav.* **1**, 1984: 301–308
- DEWHURST, W. G.—MARLEY, E.: Action of sympathomimetic and allied amines on the central nervous system of the chicken. *Br. J. Pharmacol.* **25**, 1965: 705–727
- EPSTEIN, M. L.—SHERMAN, D.—GERSHON, M. D.: Development of serotonergic neurons in the chick duodenum. *Develop. Biol.* **77**, 1980: 22–40
- ERSPAMER, V.: Fortschr. Arzneimittelforsch. **3**, 1961: 151–167
- FILECCIA, R.—MULE, F.—POSTORINO, A.—SERIO, R.—ABADESSA—URSO, S.: 5-Hydroxytryptamine involvement in the intrinsic control of oesophageal EMG activity. *Arch. int. Physiol. Biochim.* **95**, 1987: 281–288
- FREEMAN, B. M.: Is 5-hydroxytryptamine concerned in avian thermoregulation? *J. therm. Biol.* **4**, 1979: 219–221
- FREEMAN, B. M.: *Physiology and Biochemistry of the Domestic Fowl*. Volume 5, p. 414, Academic Press, London and New York, 1984, pp. 407–424
- GALLUP, G. G.—WALLNAU, L. B.—BOREN, J. L.—GAGLIARDI, G.—MASER, J. D.—EDSON, P. H.: Tryptophan and tonic immobility in chickens: Effects of dietary and systemic manipulations. *Comp. Physiol. Psychol.* **91**, 1977: 642–648
- GERSHON, M. D.—EPSTEIN, M. L.—HERGSTRAND, L.: Colonization of the chick gut by progenitors of enteric serotonergic neurons: distribution, differentiation, and maturation within the gut. *Develop. Biol.* **77**, 1980: 41–51
- GERSHON, M. D.—TAMIR, H.: Serotonectin and the family of proteins that bind serotonin. *Biochem. Pharmacol.*, **33**, 1984: 3 115–3 118
- HANIG, J. P.—AIELLO, E.—SEIFTER, J.: Permeability of the blood-brain barrier to parenteral 5-hydroxytryptamine in the neonate chick. *Eur. J. Pharmacol.* **12**, 1970: 180–182
- HANIG, J. P.—SEIFTER, J.: The effects of parenteral administration of catecholamines, serotonin and histamine on behavior and levels of these amines in the brain of the neonate chick. *Arch. int. Pharmacodyn.* **202**, 1973: 38–47
- HEHMAN, K. N.—VONDERAHE, A. R.—PETERS, J. J.: Effect of serotonin on the behavior, electrical activity in the brain, seizure threshold in the newly hatched chick. *Neurology* **11**, 1961: 1 011
- HENNIG, C. W.: Biphasic effects of serotonin on tonic immobility in domestic fowl. *Pharmacol. Biochem. Behav.*, **12**, 1980: 519–523
- HENNIG, C. W.—STEINHOFF, W. C.—BRAUGHLER, S. A.: Tonic immobility and the serotonergic system in chickens: differential blockade of receptors by cyproheptadine and cinnanserin. *Physiol. Behav.*, **44**, 1988: 15–20
- HILLMAN, P. E.—SCOTT, N. R.—van TIENHOVEN, A.: Effect of 5-hydroxytryptamine and acetylcholine on the energy budget of chickens. *Amer. J. Physiol.* **239**, 1980: R57–R61
- HOHTOLA, E.—SAARELA, S.—HARJULA, R.—HISSA, R.: Cardiovascular and thermoregulatory responses to intrahypothalamically injected neurotransmitters in the pigeon. *J. therm. Biol.* **14**, 1989: 41–45
- HUGHES, B. O.: Allelomimetic feeding in the domestic fowl. *Br. Poult. Sci.*, **12**, 1971: 359–366
- JUORIO, A. V.—VOGT, M.: Monoamines and their metabolites in avian brain. *J. Physiol.* **189**, 1967: 489–518
- LACY, M. P.—Van KREY, H. P.—DENBOW, D. N.—SIEGEL, P. B.—CHERRY, J. A.: The effects of tryptophan and tyrosine on food intake in chickens. *Poult. Sci.* **61**, 1982: 1 383
- LEE, S. R.—BRITTON, W. M.: Effect of elevated dietary tryptophan on avian hypothalamic serotonin, 5-hydroxyindole acetic acid and norepinephrine. *Poult. Sci.* **61**, 1982: 1 500

- LEIBOWITZ, S. F.—SHOR-POSNER, G.: Brain serotonin and eating behavior. *Appetite* **7**, 1986: Supplement, 1—14
- NEMOTO, N.—KAWAOI, A.—OKANO, T.—USHIYMA, H.—SATO, H.—SHIKATA, T.: Immunohistochemistry of serotonin (5-HT) in the human gut endocrine cells — An application of ultrastructural immunohistochemistry. *Acta histochem. cytochem.* **16**, 1983: 577—587
- PILOT, M. A.—THOMPSON, H. H.—ZARA, G. P.: Effect of 5-hydroxytryptamine on canine intestinal motility during fasting. *J. Physiol.* **343**, 1983: 88—89P
- POLLOCK, J. D.—ROWLAND, N.: Peripherally administered serotonin decreases food intake in rats. *Pharm. Biochem. Behav.* **15**, 1981: 179—183
- RUSBY, A. A.—ANIL, M. H.—CHATTERJEE, P.—FORBES, J. M.: Effects of intraportal infusion of glucose and lysine on food intake in intact and hepatic-vagotomized chickens. *Appetite* **9**, 1987a: 65—72
- RUSBY, A. A.—FORBES, J. M.: Effects of infusions of lysine, leucine and ammonium chloride into the hepatic vein of chickens on voluntary food intake. *Br. J. Nutrition* **58**, 1987b: 325—331
- SQUIBB, R. L.—COLLIER, G. H.: Feeding behavior of chicks under three lighting regimes. *Poult. Sci.* **58**, 1979: 641—645
- WALLACE, J. A.: An immunocytochemical study of the development of central serotonergic neurons in the chick embryo. *J. Comp. Neurol.* **236**, 1985: 443—453