Pharmacology Biochemistry & Behavior, Vol. 35, pp. 571–575. © Pergamon Press plc, 1990. Printed in the U.S.A. 0091-3057/90 $3.00 + .00

Neonatal Serotonin Reduction Alters the Adult Feminine Sexual Behaviour of Golden Hamsters

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Received 15 May 1989

JOHNSTON, H. M., A. P. PAYNE, D. P. GILMORE AND C. A. WILSON. *Neonatal serotonin reduction alters the adult feminine sexual behaviour of golden hamsters*. PHARMACOL BIOCHEM BEHAV **35**(3) 571–575, 1990.—HPLC analysis of hamster hypothalamic 5HT indicated higher levels in females than in males on day 12 after birth. Levels of 5HT and 5HIAA could be reduced in both sexes by pCPA administration. Male and female hamster pups were treated on days 1–7 or 7–14 after birth with either pCPA, 5HTP or buffer, and tested for feminine and masculine sexual behaviour in adulthood. 5HTP had no effect on behaviour in either sex. pCPA had no effect on masculine sexual behaviour nor did it affect feminine sexual behaviour when given between days 1–7. When administered on days 7–14, pCPA significantly decreased the time that females spent displaying feminine sexual behaviour, while significantly increasing it in males. We, therefore, suggest that serotonin may be modulating a neural substrate already differentiated by androgens.

Serotonin Neonate Sexual behaviour

SEXUAL dimorphism in adult social behaviour is controlled by the presence or absence of androgens during a critical perinatal period of brain development. If androgens are present, adult behavioural capacities are found to be differentiated along male lines; if absent, along female ones. Under experimental conditions this system can be manipulated to result in behavioural capacities at variance with the genetic and gonadal sex of the individual (2, 3, 9, 15, 19, 20, 23). Furthermore, many regions of the central nervous system show sexual dimorphisms in size, in neuron populations or in synaptic connections: again, these arise during the critical period as a result of the hormonal milieu at that time (1, 7, 11, 18). The mechanisms of action of steroid hormones in producing these behavioural and morphological sex differences within the developing central nervous system are less well understood. It is known that sex differences in neurotransmitter concentrations, e.g., serotonin (5HT) (17), occur in rat pups in the aftermath of the critical period. It is, however, not clear whether the difference in transmitter levels is an actual component of the differentiation process, or merely a consequence of it. The pharmacological manipulation of 5HT levels during the early postnatal period has had variable effects on adult rat behaviour and both augmentation and depletion of 5HT may have similar effects (6, 13, 23). The present study was undertaken to determine 1) If sex differences occur in hypothalamic 5HT levels during the postnatal period in another laboratory species, the golden hamster, which has been widely used in sexual differentiation studies; and 2) if manipulation of 5HT levels during the early postnatal period can alter adult sexual behaviour.

METHOD

Animals

All animals used were golden hamsters (*Mesocricetus auratus* Waterhouse) of closed colony laboratory stock established in Glasgow University Anatomy Department in 1968. The animals were housed under a reversed lighting regimen of white light (21.00–10.00 hr) and dull red light for the remainder of the day.

Experiment 1: High Performance Liquid Chromatography Analysis of Hypothalamic Indoleamines in Postnatal Pups

A total of 46 animals was used. Untreated pups of both sexes were killed by cervical dislocation on days 10 (6 males, 6 females), 12 (6 males, 6 females), 14 (6 males, 6 females), and 16 (5 males, 5 females) after birth. The brain was extracted and the

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hypothalamus was removed by making sagittal cuts on either side of the median eminence and coronal cuts 1) immediately rostral to the optic chiasm and 2) immediately rostral to the mammillary bodies [incorporating levels A48-A34 in Knigge and Joseph (16)]. The excised block of tissue produced by these cuts was divided horizontally 2–3 mm above its ventral surface and stored at −80°C until processed. Hypothalami were weighed and homogenised in 600 μl 0.1 M HCl to which 100 μg/l of internal standard, dihydroxybenzylamine (DHBA) had been added. The homogenate was centrifuged at 3000 r.p.m. for 10 min and the supernatant was injected into the chromatographic column in quantities of 20 μl; at least 2 injections per sample were analysed and any unused supernatant was stored at −80°C until required. 5-Hydroxytryptamine (5HT) and its metabolite 5-hydroxyindoleacetic acid (5HIAA) were measured by high performance liquid chromatography with electrochemical detection (HPLC-ED). The apparatus consisted of a Gilson pump and manometric unit (models 302 and 802 respectively), a Rheodyne 7125 injection valve, a 15×0.46 cm Ultrasphere ion-pair reversed-phase column (Beckman) a BioAnalytical Systems flow cell TL-5 and a LC-3A electrochemical detector. The potential was set at 0.70 V vs. an Ag/AgCl reference electrode (sensitivity 1 nA, time constant 5 sec). The output signal was measured using a Shimadzu C-RIB integrator. The mobile phase consisted of: 6.8 g/l sodium acetate; 5.75 g/l citric acid; 2.4 g/l sodium hydroxide; 0.037 g/l Na.EDTA; 0.125 g/l heptane sulphonic acid (Na salt). The pH was adjusted to 4.8 using glacial acetic acid; the methanol content was 10% and the flow rate was 1 ml/min [modified method of Siddiqui and Gilmore (21)].

Experiment 2: Confirmation of Manipulation of Postnatal 5HT by Pharmacological Means

A total of 37 animals was used. Pups received either the 5HT precursor 5-hydroxytryptophan (5HTP, 75 mg/kg) or the 5HT synthesis inhibitor p-chlorophenylalanine (pCPA, 300 mg/kg). All injections were given intraperitoneally as a 0.1 ml volume in phosphate buffer (pH 7.4). Animals received daily injections on days 7–14 after birth (for 5HTP, 10 males and 16 females; for pCPA, 5 males and 6 females) and were killed by cervical dislocation approximately 4 hours after their final injection. The tissue was processed and analysed as in Experiment 1.

Experiment 3: The Effects of Perinatal 5HT Manipulation on Adult Sexual Behaviour

A total of 219 animals was used in this experiment. The groups were treated as in Experiment 2, but a control group was included which was given phosphate buffer only. Injections were administered either on days 1–7 after birth (for 5HTP, 14 males and 15 females; for pCPA, 16 males and 25 females; for buffer-treated controls, 16 males and 25 females) or on days 7–14 after birth (for 5HTP, 15 males and 20 females; for pCPA 15 males and 18 females; for buffer-treated controls 24 males and 18 females).

As adults all animals were bilaterally gonadectomised under sodium pentabarbitone anaesthesia. Three weeks later, 5 μg oestradiol benzoate was injected subcutaneously followed 24 hours later by 500 μg progesterone. Four–six hours later the hamsters were tested for feminine sexual behaviour by placing them with a stud male for a 10-min observation period. The following data were analysed;

1) Latency to lordosis (seconds); any animals not responding were given latency scores of 600 sec.

2) Total time spent in lordosis (seconds).

3) Duration of the single longest episode of lordosis (seconds).

Following this test, all animals received injections of testosterone subcutaneously for a period of 4 weeks at a dose of 1.5 mg thrice weekly. At the end of this time each was tested with a receptive female for the display of masculine sexual behaviour during a 10-minute observation period on 3 consecutive days. The following data were analysed:

1) Latency to mount (seconds); this was the average over 3 tests.

2) Frequencies of mounting and intromission. This was the total for 3 tests.

Data were analysed by one-way ANOVA followed by intergroup comparisons using least significance difference computations using the Statgraphics program from Statistical Graphics System by Statistical Graphics Corporation.

RESULTS

Experiment 1: Postnatal Hypothalamic Amine Levels in Normal Male and Female Hamster Pups (Table 1)

5HT. Hypothalamic 5HT levels in females showed a significant variance over the postnatal days tested, $F(3,19)=8.75$, $p<0.001$. 5HT levels rose markedly between days 10 and 12 after birth and then remained fairly constant. Least significant difference (LSD) analysis showed that levels on days 12, 14 and 16 were significantly higher than on day 10 ($p<0.01$). Male hypothalamic 5HT also showed a significant variance with postnatal age, $F(3,19)=14.05$, $p<0.001$. LSD analysis showed that levels on days 14 and 16 were significantly higher than those on day 10 ($p<0.05$). Because of the different pattern of change, 5HT levels were significantly higher in females than in males on day 12 ($t=3.61$, $p<0.01$).

5HIAA. The pattern of change of hypothalamic 5HIAA was similar to that of 5HT. Thus, in females, there was a marked rise between days 10 and 12, while in males there was a more steady change with the highest rise being between days 12 and 14. For females, there was a significant overall variance between days, $F(3,19)=9.49$, $p<0.001$, with levels on days 12 and 14 being significantly higher than on day 10. For males, the change with age was less pronounced, $F(3,19)=3.31$, $p<0.04$. Females had significantly higher levels of 5HIAA than males on day 12, $t=3.63$, $p<0.01$.

Experiment 2: Pharmacological Manipulation of Hypothalamic 5HT in Neonates

Experiment 1 demonstrated that there was a sex difference in indole levels during the second week of life. As a preliminary to investigating the effects of perinatal indole manipulation on adult sexual behaviour (Experiment 3), it was necessary to verify that 5HT could be manipulated pharmacologically during this period of differentiation. Parachlorophenylalanine (a 5HT synthesis inhibitor) significantly reduced levels of 5HT and 5HIAA in both male and female pups (as expected). Conversely, 5HTP administration had a more variable effect on amine levels; while it significantly ($p<0.05$) raised 5HIAA levels in males it did not increase the amount of 5HT measured in males nor did it significantly increase levels of 5HIAA or 5HT in females (see Table 2).

Experiment 3: Sexual Behaviour of Adult Hamsters Following Postnatal 5HT Manipulation

Treatment on postnatal days 1–7. Neonatal treatment with pCPA or 5HTP on days 1–7 after birth had no significant effect on masculine or feminine sexual behaviour in adulthood in either males or females compared with buffer-treated controls.

TABLE 1

CONCENTRATION OF SEROTONIN (5HT) AND 5-HYDROXYINDOLEACETIC ACID (5HIAA) IN THE HYPOTHALAMUS OF MALE AND FEMALE HAMSTERS BETWEEN DAYS 10 AND 16 AFTER BIRTH

Age	Male (n)	Female (n)	t
5HT			
10	571 ± 146 (6)	438 ± 150 (6)	0.7, n.s.
12	896 ± 92* (6)	1555 ± 178 (6)	3.61, $p<0.01$
14	1628 ± 180 (6)	1670 ± 261 (6)	0.13, n.s.
16	1456 ± 108 (5)	1386 ± 210 (5)	0.33, n.s.
	$F(3,19)=14.05$, $p<0.001$	$F(3,19)=8.75$, $p<0.001$	
5HIAA			
10	500 ± 121 (6)	404 ± 147 (6)	0.68, n.s.
12	566 ± 55* (6)	1202 ± 184 (6)	3.63, $p<0.01$
14	854 ± 233 (6)	1480 ± 215 (6)	1.97, n.s.
16	1056 ± 59 (5)	1040 ± 48 (5)	0.26, n.s.
	$F(3,19)=3.31$, $p<0.05$	$F(3,19)=9.49$, $p<0.001$	

*Differs from female levels, $p<0.01$.
All figures are mean levels in ng/g wet wt. tissue ± SEM.

Treatment on postnatal days 7–14.

Feminine sexual behaviour in females (Table 3a). All control females (100%) adopted a lordotic posture within 60 sec of being placed with a stud male. Over 400 of the possible 600 sec of the test period were spent in lordosis and the maximum single episode of lordosis lasted on average for 240 sec. Postnatal treatment with pCPA (days 7–14) significantly increased the lordosis latency ($p<0.01$), while decreasing both the maximum time spent in lordosis ($p<0.01$) and the maximum single episode ($p<0.05$).

Postnatal 5HTP administration had no effect on adult feminine sexual behaviour in females. Although 5HTP did not raise 5HT/5HIAA levels in females, it did raise 5HIAA levels in males; therefore, behavioural studies were undertaken to determine whether this rise in 5HIAA might affect their sexual behaviour.

Feminine sexual behavior in males (Table 3b). Following priming with oestradiol and progesterone both control and experimental males assumed a lordotic posture when placed with a stud male. However, in all three groups the latency to lordosis was much greater (and both total time spent in lordosis and the maximum single episode of lordosis were much lower) than that seen in normal adult females. Postnatal pCPA administration reduced the latency to lordosis to an average of 190 sec compared with the 372 seen in normal males, but this reduction did not quite reach significance. However, the total time spent in lordosis was significantly increased in males treated with pCPA ($p<0.05$), although there was no difference in the length of the maximum single episode of lordosis.

5HTP had no effect on any aspect of feminine sexual behaviour displayed by males.

Masculine sexual behaviour in females. None of the females showed any masculine sexual behaviour in adulthood.

Masculine sexual behavior in males. Control males had a mount latency of 282 sec with an average of 26 mounts and 6 intromissions over the test period. No significant difference in any aspect of masculine sexual behaviour was found between the three treatment groups.

TABLE 2

LEVELS OF SEROTONIN (5HT) AND 5-HYDROXYINDOLEACETIC ACID (5HIAA) IN THE HYPOTHALAMUS OF 14-DAY-OLD HAMSTERS AFTER ADMINISTRATION OF p-CHLOROPHENYLALANINE (p-CPA) OR 5-HYDROXYTRYPTOPHAN (5HTP)

Amine Levels ng/g wet wt.	5HTP	pCPA	Controls	F(2,18)
Males (n)	(10)	(5)	(6)	
5HT	1351 ± 84	176 ± 146†	1628 ± 180	30.24, $p<0.001$
5HIAA	1805 ± 333*	180 ± 235†	854 ± 233	7.14, $p<0.05$
Females (n)	(16)	(6)	(6)	F(2,25)
5HT	1228 ± 84	146 ± 92†	1670 ± 261	24.02, $p<0.001$
5HIAA	1762 ± 244	180 ± 62†	1480 ± 215	8.74, $p<0.001$

*Differs from control levels, $p<0.05$.
†Differs from control levels, $p<0.01$.
See text for details. All figures are mean ng/g wet wt. of tissue ± SEM.

TABLE 3a

COMPONENTS OF FEMALE BEHAVIOUR AS SHOWN BY ADULT FEMALE HAMSTERS TREATED ON DAYS 7–14 AFTER BIRTH WITH BUFFER (CONTROLS), p-CHLOROPHENYLALANINE (pCPA) AND 5-HYDROXYTRYPTOPHAN (5HTP)

Treatment Days 7–14	Buffer	pCPA	5HTP	F(2,53)
No. of hamsters showing lordosis	18/18 (100%)	19/20 (95%)	15/18 (83%)	
Latency to lordosis (sec)	39 ± 6	182 ± 49†	64 ± 29	5.48, $p<0.01$
Total duration (sec)	414 ± 26	307 ± 44†	447 ± 27	5.19, $p<0.01$
Longest episode (sec)	241 ± 37	143 ± 34*	264 ± 37	3.29, $p<0.05$

*Differs from controls, $p<0.05$.
†Differs from controls, $p<0.01$.
See text for details. All figures are mean times (sec) ± SEM.

DISCUSSION

Sex differences in 5HT levels in the rat brain on postnatal day 12 (female levels being higher than male) have been reported by several groups (10, 14, 17, 22, 25). It has also been shown that levels could be increased in males by castration on day 1 and decreased in females by testosterone administration on the same day. Gaziri and Gladue (5) suggested that this sex difference in 5HT levels was due to a higher monoamine oxidase activity in males on day 12 and that it is the activity of this enzyme which can be altered by the presence or absence of androgens during the critical perinatal period. Our present work extends these findings by demonstrating a comparable sex difference in hypothalamic 5HT levels on day 12 in the young hamster, females having higher levels than males.

The sex difference in 5HT (and its metabolite 5HIAA) on day 12 might be part of a process of brain sexual differentiation or a result of it. If the former, one might expect that manipulation of this neurotransmitter could affect the process of sexual differentiation. Recently, Handa *et al.* (12) administered pCPA to female rats from day 8 of gestation until parturition; this resulted in the sexually dimorphic nucleus of the preoptic area (SDN-POA) in female offspring being increased in volume to that of males. Earlier, Gorski *et al.* (8) had demonstrated that postnatal androgenization of female pups also increased the volume of the SDN-POA beyond that of female controls. Thus, in the rat, reduction of 5HT levels had a similar morphological effect to that of androgenization. Can early 5HT manipulation alter adult sexual behaviour? Both Hyyppa (13) and Wilson *et al.* (25) reported that pCPA administration during the first week after birth resulted in a reduction of adult proceptive behaviour in female rats and an increase in masculine sexual behaviour in male rats. Conversely, Farabollini (4) found that perinatal pCPA had no effect on adult masculine behaviour in male rats. 5HTP administration during the first or second postnatal week had no effect on feminine sexual behaviour in male or female rats (6,25), although L-tryptophan has been reported to increase the defeminizing effect of neonatal testosterone propionate (6). In the present experiment neither pCPA nor 5HTP treatment, given over week 1 after birth, had any effect on any aspect of adult sexual behaviour in male or female hamsters, nor did 5HTP treatment during week 2 affect adult sexual behaviour in either sex. However, pCPA treatment over postnatal days 7–14 markedly reduced all aspects of feminine sexual behaviour in female hamsters, suggesting that the elevated levels of hypothalamic 5HT recorded on day 12 may play an active role in the establishment of feminine sexual behaviour patterns in

TABLE 3b

COMPONENTS OF FEMALE BEHAVIOUR AS SHOWN BY ADULT MALE HAMSTERS TREATED ON DAYS 7–14 AFTER BIRTH WITH BUFFER (CONTROLS), p-CHLOROPHENYLALANINE (pCPA) OR 5-HYDROXYTRYPTOPHAN (5HTP)

Treatment Days 7–14	Buffer	pCPA	5HTP	F(2,51)
No. of animals showing lordosis	11/24 (46%)	12/15 (80%)	10/15 (67%)	
Latency to lordosis (sec)	372 ± 52	191 ± 61	352 ± 59	2.87, n.s.
Total duration (sec)	73 ± 25	158 ± 33*	61 ± 22	3.38, $p<0.05$
Longest episode (sec)	24 ± 8	54 ± 14	28 ± 10	2.44, n.s.

*Differs from controls, $p<0.05$.
See text for details. All figures are mean times ± SEM.

the female hamster. However, a surprising result of this present experiment is that reduction of 5HT levels in the male hamster over the period of differentiation resulted in them displaying an increase in feminine sexual behaviour. Thus, a reduction in 5HT had opposite effects in the two sexes. It is possible, therefore, that 5HT acts as a "second differentiator" on a neural substrate already chiefly differentiated by androgens and that this is why the lowering of 5HT levels has produced opposite effects in the two sexes. Conversely, it may be that 5HT metabolism is different at this early stage in the two sexes. As is shown in Table 2, that males were able to metabolise excess 5HT (following 5HTP administration) to 5HIAA, may be due to their higher monoamine oxidase activity [as reported by Gaziri and Gladue (5)]. Females did not show elevated 5HT/5HIAA after 5HTP administration, suggesting that their 5HT metabolism is already at maximum capacity at this stage. There is no evidence that early 5HT manipulation can affect adult amine levels or their synthesis (4, 24, 25), although it has been reported that early hormone manipulation does (22).

Since masculine sexual behaviour was not affected by either pCPA or 5HTP treatment in either sex in the hamster, it would appear that, in this species, the neural substrates for these behavioural patterns are already established and cannot be altered via serotonergic manipulation.

In summary, our results indicate that hypothalamic 5HT levels are higher in female hamsters than in males on day 12 postnatally, as has been reported in the rat. Reduction of 5HT by pharmacological manipulation results in a reduction of time spent in lordosis in females, indicating that 5HT could play an active role in establishing feminine sexual behaviour patterns in this species. Conversely, the reduction of 5HT levels in males over this same period resulted in enhanced feminine behaviour. At present, no explanation can be found for this unexpected result.

ACKNOWLEDGEMENT

This work was partly supported by a Nuffield Foundation award to A.P.P. and C.A.W.

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