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The Influence of Ovarian Hormones on the Rat Oviductal and Uterine Concentration of Noradrenaline and 5-Hydroxytryptamine

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This paper describes the effects of estradiol and progesterone on the concentrations of noradrenaline and 5-hydroxytryptamine in the Wistar rat oviduct and uterus. The levels of noradrenaline and 5-hydroxytryptamine are higher in the oviduct than in the uterus whereas p-tyrosine and tryptophan are similar in both tissues. Estradiol treatment reduced the oviductal concentration of noradrenaline but not 5-hydroxytryptamine in oviduct, while the concentrations of both noradrenaline and 5-hydroxytryptamine were reduced in uterine horn. The levels of noradrenaline in the oviduct and uterus in rats in estrus were lower than those of diestrous rats. Bilateral ovariectomy produced an increase in uterine noradrenaline and 5-hydroxytryptamine levels. These changes were reversed in the presence of ovarian hormones as indicated by experiments where unilateral ovariectomy was performed. Reserpine administration reduced noradrenaline concentration in both the oviduct and the uterus but did not change oviductal or uterine 5-hydroxytryptamine.

These results indicate the existence of noradrenaline within postganglionic sympathetic nerve terminals and suggest that estrogens increase the utilization and the synthesis of noradrenaline in both the oviducts and the uterine horns. With respect to 5-hydroxytryptamine the data support the concept that it is mainly associated with mast cells.

KEY WORDS: Noradrenaline; 5-hydroxytryptamine; oviduct; uterus, ovariectomy.

INTRODUCTION

The noradrenaline-containing fibers that innervate the mammalian oviduct and uterus belong to the lower lumbar sympathetic system (1, 2) and there is ample evidence indicating that uterine noradrenaline decreases during the estrous phase of the sexual cycle (3–5) as well as after estradiol administration (6). Early work has shown that the number of uterine mast cells is reduced and their contents degranulated during the follicular phase of the cycle or during estrogen treatment, these changes, however, were not observed in other organs (6–8). 5-Hydroxytryptamine is also present in the uterus where it is firmly bound and presumably associated with mast cells (6, 9).

The aim of this work is to describe the effects of the administration of estradiol and progesterone and their absence (after bilateral ovariectomy) on the concentration of noradrenaline, 5-hydroxytryptamine and their precursors, *p*-tyrosine and tryptophan, in the rat oviduct and uterus. In order to obtain some information about the storage mechanisms for these amines in their locations, rats were treated with reserpine and the concen-

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tration of noradrenaline, 5-hydroxytryptamine, *p*-tyrosine and tryptophan determined.

EXPERIMENTAL PROCEDURE

Adult (220-240 g) female Wistar rats housed in an air conditioned room with controlled lighting were used. Vaginal smears from these rats were examined on 2 or 3 consecutive days and animals exhibiting the cytology for estrus (cornified epithelial cells) or diestrus (nucleated epithelial cells and leucocytes) were used.

Dissections. The rats were stunned and killed by decapitation. The oviduct and the distal portion of the uterine horns (close to the oviduct, about 1 cm long) were quickly dissected and frozen on dry ice. In addition, a portion from the duodenum about 1 cm long was dissected and frozen.

Drug treatments. Drugs were injected subcutaneously, estradiol benzoate (0.20 mg/kg) in four daily injections to rats that were killed 24 hours after the last injection. Progesterone (40 mg/kg) treatment followed the same administration schedule. Control rats were injected with the sesame oil vehicle and only those rats that were in diestrous were used. In order to maintain the animals treated with reserpine in a diestrous-like state, they were first given progesterone, 40 mg/kg in 4 days. At 24 hours before killing, these rats were treated with 0.1 or 1 mg/kg of reserpine by subcutaneous injection. Reserpine was dissolved in 50 μl of glacial acetic acid and diluted with isotonic glucose. β-estradiol 3-benzoate, progesterone and reserpine were obtained from the Sigma Chemical Company, St., Louis, MO, U.S.A.

Ovariectomies. Rats were anesthetized with intraperitoneally administered sodium pentobarbital (50 mg/kg) and either unilaterally or bilaterally ovariectomized. These rats were killed 2 weeks after the ovariectomy and the oviduct and the uterus were dissected for the chemical estimations. Any rats with remaining parts of the ovary were not included in the experiment. Control rats were subjected to anesthesia and laparotomy but the ovaries left intact.

Chemical Determinations of Amines and Aminoacids. The determinations of noradrenaline, *p*-tyrosine, 5-hydroxytryptamine and tryptophan were carried out by high performance liquid chromatography with electro-chemical detection (HPLC-ECD) as previously described (10). For the adrenaline estimations the detection potential was reduced from 0.95 V to 0.75 V but otherwise the same conditions were used. The minimum detectable amounts were 10 pg for noradrenaline, adrenaline and 5-hydroxytryptamine and 200 pg for *p*-tyrosine and tryptophan with a signal-to noise ratio of >3.

Protein Analysis. The protein concentrations were determined by the method of Lowry et al. (11), using bovine serum albumin as a standard.

Statistics. Statistical significance of the results was established by two tailed t-test or analysis of variance and Newman-Keuls multiple comparison procedure.

RESULTS

The oviductal concentration of noradrenaline in the diestrous rat ranged from 0.48 to 1.02 μg/g and in the uterus it ranged from 0.37 to 0.45 μg/g (Tables I to VI). The 5-hydroxytryptamine content in the oviduct ranged from 2.06 to 3.34 μg/g and values ranging from 0.29 to 0.57 μg/g were observed in the uterus (Tables I to VI). The concentrations of *p*-tyrosine in the oviduct and uterus ranged from 8.0 to 25.6 μg/g while in the duodenum reached higher values (63.2 μg/g) (Tables I to VI). Tryptophan concentrations ranged from 6.3 to 15.1 μg/g for the three tissues taken (Table I to VI).

The short-term chronic subcutaneous administration of estradiol benzoate produced a significant reduction in the concentration of oviductal noradrenaline (to 81% of diestrous controls) but no changes in 5-hydroxytryptamine. The concentrations of both noradrenaline and 5-hydroxytryptamine were reduced in uterine horns (to 42% and 65% of diestrous controls) (Table I). The estradiol treatment produced a moderate reduction in the *p*-tyrosine concentration in both the oviduct and uterus (to 75% and 69% of diestrous controls, respectively). No changes in tryptophan levels were observed in either tissue (Table I). These changes were observed after calculation of the results in μg/g of fresh tissue or ng/mg of protein (Table I). If the concentrations are expressed in ng/organ, the decreases in noradrenaline content are observed for the uterus of estradiol treated rats (to 66% of diestrous controls) but no changes were observed for the oviduct (results not shown). Short-term chronic progesterone administration produced a small increase in the concentration of oviductal *p*-tyrosine but no further changes either in the oviduct or the uterus (Table II).

Rats killed in the estrous phase of the cycle showed a significant reduction in the concentration of noradrenaline in both the oviduct and the uterus (to 63% and 57% of their respective diestrous controls) (Table III). The concentrations of *p*-tyrosine, 5-hydroxytryptamine and tryptophan in both the oviduct and the uterus were not different from their respective diestrous controls (Table III).

Bilateral ovariectomy reduced the concentration of noradrenaline in the oviduct to 46% of the sham operated controls, in the presence of an increase in both noradrenaline and 5-hydroxytryptamine in the uterine horns to 195% and 279% of their respective control (Table IV). The excision of one ovary produced a reduction in both noradrenaline and 5-hydroxytryptamine in the ipsilateral oviduct (to 38% and 66% of their respective contralateral controls) and a reduction of noradrenaline in the ipsilateral uterine horn while the concentration of 5-hydroxytryptamine was increased (Table V).

Attempts to determine the concentration of adrenaline in the rat oviduct or uterus showed that, if present, the levels are below the limits of sensitivity of the HPLC-ECD method employed (<0.02 μg/g of fresh tissue).

As would be expected, the administration of reserpine (0.1 or 1 mg/kg) to progesterone-treated rats produced dose-dependent significant reductions in the

Table I. Effect of the Chronic Administration of Estradiol (0.20 mg/kg in 4 Days) on the Concentration of Noradrenaline (NA), *p*-Tyrosine, 5-Hydroxytryptamine (5-HT), and Tryptophan on the Rat Oviducts and Uterine Horns

	Diestrous Controls		Estradiol	Percentage of Controls
		Oviducts		
	μg/g		μg/g	
NA	0.74 ± 0.03 (15)		0.60 ± 0.02 (16)**	81
p-Tyrosine	14.4 ± 0.91 (15)		10.8 ± 0.51 (16)*	75
5-HT	2.93 ± 0.20 (14)		2.83 ± 0.24 (15)	97
Tryptophan	11.0 ± 0.72 (15)		10.9 ± 0.57 (16)	99
	ng/mg of protein		ng/mg of protein	
NA	8.80 ± 0.40 (15)		7.10 ± 0.40 (16)*	81
p-Tyrosine	175.0 ± 11.0 (15)		125.0 ± 5.00 (16)**	71
5-HT	35.0 ± 2.0 (14)		35.0 ± 4.00 (15)	100
Tyrptophan	132.0 ± 9.0 (15)		156.0 ± 6.80 (16)	118
		Uterine Horns		
	μg/g		μg/g	
NA	0.38 ± 0.02 (15)		0.16 ± 0.02 (15)**	42
p-Tyrosine	16.0 ± 1.12 (15)		11.1 ± 0.56 (16)**	69
5-HT	0.48 ± 0.04 (12)		0.31 ± 0.03 (15)*	65
Tyrptophan	12.6 ± 0.51 (15)		11.0 ± 0.58 (16)	87
	ng/mg of protein		ng/mg of protein	
NA	4.80 ± 0.30 (15)		2.30 ± 0.30 (15)**	48
p-Tyrosine	200 ± 15.0 (15)		150 ± 9.00 (15)*	75
5-HT	6.10 ± 0.60 (12)		4.10 ± 0.40 (15)*	67
Tyrptophan	160 ± 7.50 (15)		150 ± 8.80 (15)	94

The concentrations are means (± standard error of the mean), number of determinations in brackets in μg/g of fresh tissue or ng/mg of protein. Student's *t*-test * $P < 0.01$; ** $P < 0.001$.

Table II. Effect of the Chronic Administration of Progesterone (40 mg/kg in 4 days) on the Concentration of Noradrenaline (NA), *p*-Tyrosine, 5-Hydroxytryptamine (5-HT) and Tryptophan on the Rat Oviducts and Uterine Horns

	Diestrous Controls		Progesterone	Percentage of Controls
		Oviduct		
	μg/g		μg/g	
NA	0.66 ± 0.05 (15)		0.76 ± 0.05 (15)	115
p-Tyrosine	14.8 ± 0.78 (15)		17.2 ± 0.71 (16)*	116
5-HT	3.34 ± 0.31 (14)		2.89 ± 0.23 (16)	87
Tryptophan	12.1 ± 0.51 (15)		12.7 ± 0.54 (16)	105
		Uterine horns		
NA	0.38 ± 0.04 (12)		0.30 ± 0.02 (15)	79
p-Tyrosine	16.6 ± 1.22 (15)		17.6 ± 0.68 (16)	106
5-HT	0.57 ± 0.06 (15)		0.46 ± 0.05 (14)	81
Tryptophan	12.9 ± 0.43 (15)		13.6 ± 0.30 (16)	105

The concentrations are means (± standard error of the mean), number of determinations in brackets in μg/g of fresh tissue or ng/mg of protein. Student's *t*-test * $P < 0.05$.

concentrations of oviductal, uterine and duodenal noradrenaline (Table VI). In contrast, reserpine induced no change in the concentration of 5-dydroxytryptamine (Table VI) in any of the three tissues investigated. The higher dose of reserpine (1 mg/kg) significantly increased oviductal and uterine *p*-tyrosine levels while the lower dose (0.1 mg/kg) increased only the uterine levels; in contrast, both reserpine doses reduced duodenal *p*-tyrosine (Table VI). The uterine or duodenal tryptophan levels were not affected by the reserpine treatment but a small increase was observed in the oviduct following the administration of the higher dose (Table VI).

Table III. The Concentration of Noradrenaline (NA), *p*-Tyrosine, 5-Hydroxytryptamine (5-HT) and Tryptophan in the Oviducts and Uterine Horns of Rats in Estrous and Diestrous

	Diestrous Controls	Estrous	Percentage of Controls
	Oviduct		
	μg/g	μg/g	
NA	0.48 ± 0.02 (14)	0.30 ± 0.02 (8)*	63
p-Tyrosine	8.01 ± 0.40 (14)	8.42 ± 0.54 (8)	105
5-HT	3.28 ± 0.24 (14)	3.60 ± 0.25 (8)	110
Trytophan	6.27 ± 0.66 (12)	7.18 ± 0.26 (8)	115
	ng/mg of protein	ng/mg of protein	
NA	7.40 ± 0.40 (14)	4.50 ± 0.35 (8)*	61
p-Tyrosine	126 ± 8.00 (14)	125 ± 9.00 (8)	99
5-HT	51.0 ± 4.10 (14)	53.0 ± 3.90 (8)	104
Tryptophan	112 ± 6.00 (12)	94 ± 11 (8)	84
	Uterine horns		
	μg/g	μg/g	
NA	0.37 ± 0.02 (14)	0.21 ± 0.02 (15)*	57
p-Tyrosine	9.06 ± 0.61 (14)	11.1 ± 0.95 (14)	123
5-HT	0.51 ± 0.04 (14)	0.50 ± 0.07 (13)	98
Tryptophan	8.97 ± 0.17 (14)	8.96 ± 0.54 (14)	100
	ng/mg of protein	ng/mg of protein	
NA	5.00 ± 0.40 (14)	2.80 ± 0.30 (15)*	56
p-Tyrosine	126 ± 8.00 (14)	141 ± 11.0 (14)	112
5-HT	7.10 ± 0.60 (14)	6.40 ± 0.80 (13)	90
Tryptophan	125 ± 5.00 (14)	114 ± 6.00 (14)	91

The concentrations are means (± standard error of the mean), number of determinations in brackets in μg/g of fresh tissue or ng/mg of protein. Student's *t*-test * $P < 0.001$.

Table IV. The Effect of Bilateral Ovariectomy on the Concentration of Noradrenaline (NA), *p*-Tyrosine, 5-Hydroxytryptamine (5-HT) and Tryptophan on the Rat Oviducts and Uterine Horns

	Diestrous Controls	Ovariectomy	Percentage of Controls
	Oviducts		
	μg/g	μg/g	
NA	0.81 ± 0.04 (17)	0.37 ± 0.04 (17)**	46
p-Tyrosine	19.3 ± 1.66 (15)	20.7 ± 1.68 (17)	107
5-HT	2.06 ± 0.20 (17)	1.75 ± 0.21 (17)	85
Tryptophan	13.2 ± 0.42 (17)	13.0 ± 0.54 (17)	99
	Uterine horns		
NA	0.41 ± 0.04 (14)	0.80 ± 0.09 (11)**	195
p-Tyrosine	25.6 ± 1.81 (14)	21.6 ± 1.97 (11)	84
5-HT	0.29 ± 0.03 (14)	0.81 ± 0.16 (11)*	279
Tryptophan	15.1 ± 0.390 (14)	13.5 ± 0.55 (11)	89

The concentrations are means (± standard error of the mean), number of determinations in brackets in μg/g of fresh tissue. Student's *t*-test * $P < 0.01$; ** $P < 0.001$.

DISCUSSION

It has been known for quite some time that rat uterine noradrenaline decreases during estrus (3–5) or following estradiol administration (6). The present experiments shows that similar changes occur in the rat oviduct and uterus either after chronic estradiol administration or during estrus (Table I and III). The fact that the reductions in uterine noradrenaline were observed after expressing the results as μg/g of fresh tissue, ng/mg of protein or mg/uterus suggests that estrous rats exhibit a reduced noradrenaline innervation and that they are not the consequence of increase in water content and/or protein synthesis that concurrently occur during estrus. Similar reductions have been observed with respect to noradrenaline content in the guinea-pig uterus during

Table V. The Effect of Unilateral Ovariectomy on the Ipsilateral Concentration of Noradrenaline (NA), *p*-tyrosine, 5-Hydroxytryptamine (5-HT) and Tryptophan on the Rat Oviducts and Uterine Horns

	Intact	Ovariectomy	Percentage of Controls
		Oviducts	
	μg/g	μg/g	
NA	1.02 ± 0.04 (8)	0.39 ± 0.10 (8)*	38
p-Tyrosine	19.0 ± 2.22 (8)	14.8 ± 1.31 (8)	78
5-HT	2.51 ± 0.36 (8)	1.65 ± 0.20 (8)*	66
Tryptophan	12.8 ± 1.04 (8)	11.2 ± 0.97 (8)	88
		Uterine horns	
NA	0.45 ± 0.08 (8)	0.35 ± 0.09 (8)*	78
p-Tyrosine	19.4 ± 2.28 (8)	19.1 ± 1.87 (8)	99
5-HT	0.38 ± 0.08 (8)	0.48 ± 0.09 (8)*	126
Tryptophan	13.8 ± 0.95 (8)	13.6 ± 0.83 (7)	99

The concentrations are means (± standard error of the mean), number of determinations in brackets in μg/g of fresh tissue. Student's paired *t*-test * $P < 0.01$.

Table VI. The Effect of the Subcutaneous Administration of Reserpine on the Concentration of Noradrenaline (NA), *p*-Tyrosine, 5-hydroxytryptamine (5-HT) and Tryptophan on the Rat Oviducts, Uterine Horns, and Duodenum

	Vehicle	0.1 mg/kg	1 mg/kg
		Oviduct	μg/g
	μg/g	μg/g	
NA	0.90 ± 0.06	0.43 ± 0.05**	0.19 ± 0.04**
p-Tyrosine	16.0 ± 0.99	21.8 ± 2.28	30.3 ± 3.00**
5-HT	3.32 ± 0.47	2.90 ± 0.21	2.64 ± 0.43
Tryptophan	10.2 ± 0.56	11.7 ± 0.73	12.9 ± 0.41**
		Uterine horns	
NA	0.44 ± 0.02	0.14 ± 0.02**	< 0.05
p-Tyrosine	16.7 ± 0.95	21.5 ± 1.37*	23.9 ± 1.79**
5-HT	0.56 ± 0.06	0.50 ± 0.09	0.52 ± 0.08
Tryptophan	14.6 ± 1.19	13.6 ± 0.47	15.3 ± 0.38
		Duodenum	
NA	0.65 ± 0.07	0.13 ± 0.04**	0.020 ± 0.002**
p-Tyrosine	63.2 ± 7.67	45.5 ± 3.49*	41.5 ± 3.67*
5-HT	7.58 ± 0.88	7.76 ± 0.82	8.80 ± 0.37
Tryptophan	17.1 ± 2.08	14.2 ± 1.30	13.8 ± 0.95

All rats were chronically pretreated with progesterone (40 mg/kg in 4 days). Reserpine was given 24 hours before killing the animals. The concentrations are means (± standard error of the mean) calculated from 7 determinations in μg/g of fresh tissue. Significances were estimated by one-way analysis of variance and multiple comparison by the Newman-Keuls test; * $P < 0.05$, ** $P < 0.01$.

estrus (12). Both of these findings are at variance with some earlier observations in the rabbit oviduct and uterus where chronic administration of estradiol produced an ncrease in total noradrenaline content (13–15). It is worth pointing out, however, that if these concentrations are re-calculated as μg/g of fresh tissue (13–15), they show either no change or a reduction in noradrenaline content (also see reference 16). In contrast to the rat oviductal and uterine noradrenaline reductions, no changes were observed in the level of tryptophan either during estrus or as the result of the administration of estradiol (Tables I and III).

The finding that both bilateral and unilateral ovariectomy cause similar reductions in oviductal noradrenaline concentration (Table IV and V) indicated that the changes are unrelated to presence of ovarian hormones but most likely the consequence of damage to the adrenergic innervation inflicted during the ovariectomy. It is most likely that these reductions occur by lesion of the long noradrenergic fibers originating from the lower lumbar sympathetic system (1) where at least part of the remaining noradrenaline is located within the system of short adrenergic fibers (17, 18). In contrast, the doubling in uterine noradrenaline concentration following bilateral ovariectomy (Table IV) is not observed in unilaterally ovariectomized rats (Table V) pointing to an interaction between ovarian hormones and noradrenaline concentration. These changes are in agreement with the decreases observed in uterine noradrenaline after estradiol administration (Table I) and probably are effected through the system of short adrenergic fibers that are very sensitive to the effects of ovarian hormones (17, 18). These findings are in apparent disagreement with those of an earlier publication where ovariectomy produced no changes in uterine content (ng/organ) or noradrenaline (19); if Falck's group values are re-calculated as μg/g, an increase in rat uterine noradrenaline concentration is observed.

Noradrenaline is formed from *p*-tyrosine by hydroxylation in the *m*-phenyl and β-side chain positions (for a review see reference 20). Both the oviduct and the uterus in the diestrous phase of the sexual cycle contain *p*-tyrosine and its concentration is significantly reduced in both tissues after estradiol administration (Table I). These changes occur simultaneously with a decrease in noradrenaline suggesting that estradiol lowers noradrenaline turnover rate. Progesterone administration increases oviductal *p*-tyrosine and though the levels of noradrenaline are somewhat increased by this treatment, the increase does not reach significance (Table II). The rat oviductal or uterine concentrations of *p*-tyrosine were not changed in estrous (Table III) or following ovariectomy (Tables IV and V).

An earlier publication has shown that the rat uterus contains 0.10 μg/g of 5-hydroxytryptamine (state of sexual cycle not indicated) and this level is reduced following estradiol administration (6). The present investigation confirms that 5-hydroxytryptamine concentrations are reduced following estradiol treatment (Table I) but differ in that the endogenous levels of 5-hydroxytryptamine are 3-5 times higher than those reported by Mc Kercher **et al.** (6) (Tables I through to VI). A possible cause for these difference in concentration may reside in the different rat strains used in two series of experiments. In addition, this investigation further demonstrates that in diestrous rats, 5-hydroxytryptamine levels are higher in the oviduct (2.0-3.3 μg/g) than in the uterus (0.30-0.51 μg/g) (Tables I to VI). The 5-hydroxytryptamine levels in both tissues are reduced after estradiol administration (Table I) but are not changed during estrous in normally cycling rats (Table III) nor after progesterone administration (Table II).

The levels of 5-hydroxytryptamine in the uterus of bilaterally ovariectomized rats are about three times those of diestrous controls (Table IV), an effect that is not observed following unilateral ovariectomy (Table V). This suggests that, as is the case for noradrenaline, the presence of ovarian hormones also influence the levels of 5-hydroxytryptamine in the uterus. The moderate reduction in oviductal 5-dydroxytryptamine following unilateral ovariectomy (Table V) remains unexplained by the present experiments.

It has been known for many years that the 5-hydroxytryptamine contained in the chromaffin cell system is resistant to the effect of doses of reserpine that are quite effective in depleting noradrenaline (21, 22). In the rat oviduct, uterus and duodenum noradrenaline is markedly reduced by the reserpine treatment while the concentrations of 5-hydroxytryptamine are not changed (Table VI). The findings are consistent with the existence of noradrenaline in granules within postganglionic sympathetic fibers and 5-hydroxytryptamine in mast cells. It should be noted that as has been observed already in the brain (23), reserpine treatment, also increases the *p*-tyrosine levels in both the oviduct and the uterus. Surprisingly, the opposite effect was observed in the duodenum which was shown to contain substantially more *p*-tyrosine than either the oviduct or the uterus (Table VI). This suggests the existence of a difference in the metabolism of the aminoacid between these tissues. In parallel to its effects in the brain (23), oviductal tryptophan is increased after reserpine treatment.

The results suggest that estrogens decrease noradrenaline concentrations (Table II), it remains to be elucidated whether the decrease occurs after reduction in noradrenaline synthesis or increase in its metabolism. The oviduct and the uterus contain 5-hydroxytryptamine which may be associated with mast cells.

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