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RELATIONSHIP BETWEEN GONADAL DEVELOPMENT AND RADIATION SENSITIVITY IN THE FEMALE GOLDEN HAMSTER*

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ABSTRACT

N. H. Chao, aud E. W. Hupp (1972) *Relatinship Between Gonadal Development and Radiation Sensitivity in the Female Golden Hamster*, Bull. Inst. Zool., Academia Sinica **11**(2): 1-10. Female golden hamsters were irradiated with x-rays (220 R) 13 and 15-day prenatally and 1-, 3-, 6-, 8-, 11-, 15-, and 22-day postnatally. Mean ovarian weights were greatly suppressed in all irradiated female hamsters. The least suppressed group was those irradiated 22-day postnatally. Ovarian weights of hamsters irradiated 13- and 15-day prenatally, and 11-day postnatally were most adversely affected. Two periods of increased sensitivity were indicated by the reduction in total number of corpus lutea and follicles. One was at day 15 of prenatal life, the other sensitive period was at days 8, 11, and 15 of postnatal life. The greatest effect was seen in the female hamsters irradiated 11-day postnatally. There was a low correlation ($r=0.30$) between ovarian weight and the total number of follicles and corpus lutea.

All groups of irradiated female hamsters averaged less growing follicles than the control group except those irradiated 13-day prenatally. The control group had the greatest number of primordial follicles. Only in groups irradiated 1- and 8-day postnatally were corpus lutea dominant. Vesicular follicles and empty follicles were in the minority.

Fetal and neonatal hamsters were killed on the proper days for the study on normal development. The present results indicate that there is a relationship between the qualitative and quantitative changes in the ovaries with increasing age and radiosensitivity. Maximum radiosensitivity in the female coincided with the completion of organization of follicular cells around all of the oocytes, the appearance of rapidly growing follicles, and also a rapid increase in the total size of the ovary. However, the morphology of the oocytes themselves appeared to be similar in stages preceding and following the period of highest sensitivity.

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Studies of the effects of irradiation on the gonads of mammals have been largely restricted to the rat and mouse. Recently, use of the hamster as an experimental animal has increased. The first objective of this research was to establish the radiosensitivity pattern of female hamsters. The second objective was to determine through quantitative and qualitative observations of the non-irradiated fetal and neonatal ovaries if changes in the radiosensitivity of germ cells could be correlated with stages of major change in morphogenesis.

MATERIALS AND METHODS

Random-bred golden hamsters were ordered from the Lakeview Hamster Colony, Newfield, New Jersey, U. S. A. They were maintained in an animal room in which temperature and light were controlled (75°F, and 12-hour light, 12-hour dark), and were fed Wayne Lab-Blox and water, *ad libitum*.

Female hamsters were mated and checked daily for litters. Postnatally irradiated hamsters were obtained by irradiating the litters at each proper day. Prenatally irradiated hamsters were obtained by irradiating the pregnant females of a known stage of gestation. A 250 KV General Electric Therapy Unit was used as a source of radiation. The unit operated at 250 kVp at 15 ma, with 0.5 mm copper and 1.0 mm aluminum filtration. The target-to-subject distance was adjusted to obtain a dose rate of 55 R per minute, totalling 220 R for four minutes.

For the fertility test, females from each treatment group were placed with males of known fertility (one male was placed with two females) for 10 days. Females were then moved to littering cages to litter and rear their young to weaning. Each female was allowed to rear up to four litters, but if she failed to litter following three 10-day mating periods, she was classified sterile and not tested further. Ovaries were obtained for weighing and histological analysis following weaning of the fourth litter or when the female was classified sterile. Controls were handled in a like manner except they were not irradiated.

Sectioning and analyzing of the ovaries of control and irradiated hamsters killed at 50 days of age were done. A cross-section of one ovary from each female was observed by using the binocular microscope and the number of corpus lutea and follicles in different stages were counted and recorded. The system of classification of empty follicle, primordial follicle, growing follicle, vesicular follicle, and corpus luteum will be described in the result section. With the objective to relate radiosensitivity to the normal development of fetal and neonatal hamsters, two female hamsters were killed at ages similar to that at which radiation was applied. Histological serial sections were prepared and treated as above. Polaroid pictures were taken to aid in the comparisons between the various stages of development. Statistical analysis, using Duncan's multiple range test and Chi square computation, was applied to weights and counts of follicle and corpus luteum to aid in interpretation of the results obtained[10].

RESULTS

Ovarian weight:

Ovarian weights were greatly suppressed in all irradiated females (Table I). However, statistical analysis showed that the mean ovarian weight in all irradiated groups except those irradiated 13-day prenatally and 11-day postnatally did not differ from the control group at the 5% level of significance. The irradiated groups did not differ from each other at the 5% level of significance. The least suppressed group was that irradiated 22-day postnatally with a mean ovarian weight of 49.6 mg which was 58.8% of control weight.

The control group had the largest standard deviation of the ovarian weight. Ovarian weights of the irradiated hamsters were more constant than those of the controls. This was probably due to reduced numbers of follicles and corpus lutea whose growth and regression caused greater variability in weight of control ovaries. Ovarian

TABLE I

Ovarian Weights of Hamsters X-Irradiated with 220 R and Killed at 50 Days of Age

Treatment	Mean ± Standard Deviation** (mg.)	Percent of Control (%)
Control	84.9±42.2 a*	100.0
Day irradiated		
13 Prenatal	30.3± 5.7 b	35.3
15 Prenatal	38.6± 8.7 ab	45.9
1 Postnatal	41.4±14.4 ab	58.2
3 Postnatal	39.3± 5.8 ab	45.9
6 Postnatal	46.0±10.5 ab	54.1
8 Postnatal	41.8± 7.2 ab	49.4
11 Postnatal	32.1± 6.4 b	37.7
15 Postnatal	39.8± 5.7 ab	47.1
22 Postnatal	49.6± 7.3 ab	58.8

* Means with the same superscript do not differ at the 5% level of significance.
** N=10

weights of hamsters irradiated 1-day postnatally varied from 20 mg to 71 mg, those of other irradiated groups varied within smaller ranges.

Histological analysis of ovary sections:

In the present paper, the method for classification of irradiated follicles followed a similar pattern to that of Erickson[8,9] for cattle and Teng[15] for goats.

An *Empty follicle* consists of one layer of follicular cells but without an oocyte in the center.

A *Primordial follicle* is an oocyte surrounded by a single layer of follicular cells.

A *Growing follicle* is an oocyte with two or more layers of follicular cells, but without a vesicle.

A *Vesicular follicle* is an oocyte with a nearly or fully formed vesicle.

A *Corpus luteum* is full of lutein granular cells but no oocyte, since it has been expelled.

These five classes were determined microscopically. The number in each class was recorded.

All irradiated groups averaged less than the control group in total number of corpus lutea and follicles except those irradiated 13-day prenatally (Table II). The mean total numbers of corpus lutea and follicles of irradiated groups differed from the control group at the 5% level of significance except for those irradiated 13-day prenatally and 3-day postnatally. The animals irradiated 11- and 15-day postnatally had the minimum mean number of corpus lutea and follicles.

Two periods of increased sensitivity are indicated by the number of corpus lutea and follicles (Fig. 1). There was a sensitive period at 15-day of prenatal life. Increased number of corpus lutea and follicles observed in materials irradiated 1- and 3-day postnatally indicated increment of resistance during this period. However, at 6-day of postnatal life, the sensitivity increased again, leading to a very sensitive period at 8-, 11-, and 15-day of postnatal life. Following this sensitive period, increased resistance was shown by the increased mean number of corpus lutea and follicles in materials irradiated 22-day postnatally. The greatest effect was seen in

TABLE II

Mean and Standard Deviation of Total Numbers of Corpus Lutea and Follicles in one Ovary Section of Hamsters X-Irradiated with 220 R and Killed at 50 Days of Age

Treatment	Mean ± Standard Deviation** (no.)	Percent of Control (%)
Control	32.6±19.4 ab*	100.0
Day Irradiated		
13 Prenatal	36.6±15.3 a	112.1
15 Prenatal	18.3± 9.6 def	54.6
1 Postnatal	25.8±10.8 bcd	78.8
3 Postnatal	31.9±12.7 abc	97.0
6 Postnatal	20.1±10.8 de	60.6
8 Postnatal	15.6± 7.4 def	48.5
11 Postnatal	9.7± 9.8 f	30.3
15 Postnatal	10.4± 3.4 ef	30.3
22 Postnatal	22.2± 8.5 cd	66.7

* Means with the same superscript do not differ at the 5% level of significance.
** N=10

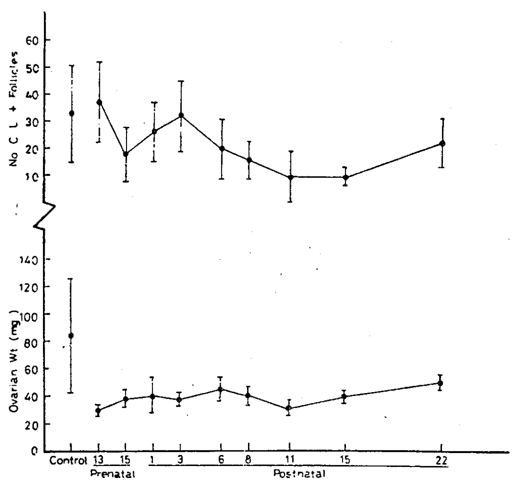

Fig. 1. Comparison of Means and Standard Deviation of Ovarian Weight and Total Number of Corpus Lutea (C. L.) and Follicles of Hamsters X-Irradiated with 220 R and Killed at 50 Days of Age.

females irradiated 11- and 15-day postnatally where only 30 and 32% respectively, as many follicles and corpus lutea were observed as in control hamsters. Ovaries irradiated 11-day postnatally had the most adversely affected ovarian weight and also the smallest mean number of corpus lutea and follicles. Nevertheless, there was a low correlation ($r=0.30$) between ovarian weight and the number of follicles and corpus lutea (Fig. 1).

Only two groups, those irradiated 13-day prenatally and 3-day postnatally had mean total numbers of follicles and corpus lutea which did not differ from the control group. All irradiated groups had less growing follicles than the control group except those irradiated 13-day prenatally (Table III). The control group had the greatest number of primordial follicles. In the control group and groups irradiated 3- and 15-day postnatally, primordial follicles were dominant. In the groups irradiated on 13- and 15-day prenatally and 6-, 11-, and 22-day postnatally, the majority were growing follicles. Only in groups irradiated 1- and 8-day postnatally life were corpus lutea dominant. Vesicular follicles and empty follicles were in the minority (Table IV).

TABLE III

Mean and Standard Deviation of Number of Corpus Lutea and Follicles in one Ovary Section of Hamsters X-Irradiated with 220 R and Killed at 50 Days of Age

Treatment	Corpus Lutea	Vesicular Follicles	Growing Follicles	Primordial Follicles	Empty Follicles
Control	7.2±7.4	0.3±0.5	12.3±8.7	14.0±12.1	0.5±0.3
Day Irradiated					
13 Prenatal	9.6±3.3	0.3±0.5	16.3±8.4	10.1± 8.4	0.3±0.9
15 Prenatal	5.7±3.6	0.7±0.7	6.3±4.9	5.7± 9.2	0.0±0.0
1 Postnatal	9.0±4.2	1.2±2.1	6.8±3.8	8.7± 5.3	0.1±0.3
3 Postnatal	9.0±2.8	0.8±0.9	10.7±5.7	11.1± 8.6	0.3±0.7
6 Postnatal	6.7±3.7	0.9±1.0	7.8±4.5	4.2± 4.3	0.5±1.1
8 Postnatal	6.7±2.7	0.7±0.7	5.8±4.7	1.8± 1.8	0.6±1.9
11 Postnatal	3.4±4.7	0.1±0.3	3.9±4.8	2.2± 2.4	0.1±0.3
15 Postnatal	2.3±2.1	0.1±0.3	3.2±3.2	4.2± 2.2	0.5±0.8
22 Postnatal	6.4±3.2	0.5±0.7	11.5±4.6	4.0± 1.6	0.9±1.9

TABLE IV

Percentage of Corpus Lutea and Follicles in one Ovary Section of Hamsters X-Irradiated with 220 R and Killed at 50 Days of Age

Treatment	Corpus Lutea (%)	Vesicular Follicles (%)	Growing Follicles (%)	Primordial Follicles (%)	Empty Follicles (%)
Control	21.0	0.9	35.9	40.8	1.5
Day Irradiated					
13 Prenatal	26.2	0.8	44.6	27.6	0.8
15 Prenatal	30.9	3.6	34.6	30.9	0.0
1 Postnatal	34.9	4.7	26.4	33.7	0.4
3 Postnatal	28.2	2.5	33.6	34.8	0.9
6 Postnatal	33.3	4.5	38.8	20.9	2.5
8 Postnatal	43.0	4.5	37.2	11.5	3.9
11 Postnatal	35.1	1.0	40.2	22.7	1.0
15 Postnatal	22.3	1.0	31.1	40.9	4.9
22 Postnatal	27.5	2.2	49.4	17.2	3.9

The present results demonstrate that the pattern of radiation damage in female germ cells is evident at 50 days of age. Exposure to 220 R results in a depletion of germ cells at most stages irradiated, with a nearly equal depletion of all types of follicles[11,12].

Results of fertility tests:

The results of the fertility tests summarized in Table V closely parallel those of ovarian weight and histological analysis of animals killed

TABLE V

Number of Fertile Females and Mean Number of Offspring Born Per Female Tested

Treatment	Number of Females		Mean Number Born Per Female in Litter				Total Born Per Female**
	Tested	Fertile*	1	2	3	4	
Control	13	12	2.9	8.5	3.3	4.1	18.9
Day Irradiated							
13 Prenatal	5	4	5.0	0	0	—	5.0
1 Postnatal	8	8	6.5	4.9	7.8	3.1	22.2
3 Postnatal	13	7	2.1	1.8	3.2	3.8	10.9
5 Postnatal	12	10	5.6	3.6	5.5	2.6	17.2
7 Postnatal	13	8	2.6	1.3	1.5	1.5	6.9
10 Postnatal	16	6	2.4	0	0	—	2.4
14 Postnatal	10	1	0	0.6	0.4	0	1.0
18 Postnatal	16	8	1.5	1.9	1.7	0	5.1
22 Postnatal	13	11	3.6	5.7	3.2	1.8	14.2

* Number of females that had one or more litters.

** Calculated on basis of total offspring in 4 possible litters/number of females tested.

at 50 days of age. Total offspring produced per irradiated female was significantly less in all irradiated groups except those irradiated 1-day postnatally (chi-square analysis, 5% level of significance). The greatest effect was seen in animals irradiated on day 14 where only 1 of 10 females produced any offspring; animals irradiated on 7-, 10-, and 18-day postnatally and 13-day prenatally also exhibited very adverse effects on productivity. The reduction in productivity was due both to decreased numbers of females littering and to reduced litter size in the second and subsequent litters produced.

Radiation effect was greater in second, third, and fourth litters than the first. This is in agreement with the findings of Krohn[14], as exposure of the rats to ionizing radiation accelerates the rate of loss of oocytes from the ovary indicating that the irradiated females utilized the limited number of oocytes that they had for the first few litters and then became sterile when the supply was exhausted. Histological examination of the ovaries from the fertility-tested females supported this conclusion. Very few germinal elements remained in the ovaries of irradiated females examined; the numbers were so low that quantitative counts were not made. Ovarian weights obtained at the end of the fertility tests, when expressed as percent of control, were very similar to those obtained from animals killed at 50 days of age.

Normal ovarian developments:

Extremely rapid change in the developing ovaries was observed[4]. The ovaries of early developing hamsters at 13-day of prenatal life were characterized by microscopically distinguishable somatic and germinal elements in a random arrangement, while advanced stages of developing follicles were found at 22-day of postnatal life.

Day 13 Prenatal

Internal organization was absent in the ovary. Somatic and germinal elements were distinguishable microscopically, but appeared to be in a random arrangement.

Day 15 Prenatal

In the gonad, germinal elements were dominant. Mitotic figures were found but they were not as numerous as at 1-day of postnatal life. In some cases, there appeared to be primary organization of the sex cords.

Day 1 Postnatal

Typical sex cords were apparent. The proportion of germinal elements was high. Numerous mitotic figures were observed. Some cells appeared to have proceeded to the dictyate stage of meiosis, similar to oocytes at later stages of development of the organism, however, many of the nuclei appeared slightly smaller than at later stages.

Day 3 Postnatal

In some cases the outlines of the sex cord were still visible. In other areas, the organization had disappeared. Most of the germinal elements had been transformed into the dictyate stage of meiosis, but some mitotic activity in the germinal elements was still visible.

Day 5 Postnatal

Ovigenous cords were absent. The gonad had increased in size, oocytes were in high proportion, but the size of oocytes still seemed slightly smaller than later stages. Nucleoli were prominent indicating that oocytes had the same general conformation as observed later. No mitotic figures were observed.

Day 7 Postnatal

Cells in the central part of the gonad were arranged in cords. Newly differentiated oocytes lay beneath the ovarian surface epithelium. In many cases, "nests" of several oocytes were close together. No follicles had yet formed.

Day 10 Postnatal

In the medulla there were many primordial follicles with a single layer of cubodial granulosa cells and a few growing follicles with not more than two layers of granulosa cells. The majority of growing follicles were in the center while the primordial ones distributed throughout the cortex. The oocytes that were in stage before primordial follicles were present beneath the surface epithelium and they were slightly smaller than the oocytes in the follicles.

Day 14 Postnatal

Primordial follicles were distributed throughout the entire cortex. Many growing follicles with two to three layers of granulosa cells, which were greater in size than those seen at 10 days of age, were observed.

Day 18 Postnatal

The ovary had increased in size again and growing follicles increased in number and size. Most growing follicles in this stage possessed three or more layers of granulosa cells. Primordial follicles could only be found in the peripheral zone.

Day 22 Postnatal

This stage was distinguished by increase in size of ovary as well as increase in size, number, and layers of granulosa cells of growing follicles. The oocytes in growing follicles had not increased much in size since 10-day of postnatal life. Primordial follicles were located in the peripheral zone.

DISCUSSION

Ovarian weights were all suppressed differentially by radiation in this study. The smallest mean ovarian weight and the least suppressed ovarian weight were 35% and 59% of the control respectively. Hupp *et al.*[18] noted a mild suppression in ovarian weights in female rats irradiated 14- and 16-day prenatally and a severe effect, as measured by ovarian weight and fertility, in females irradiated on days 5 through 17 of postnatal life. In the present work, it was also found that the female hamsters irradiated 13-day prenatally as well as 11-day postnatally had apparent suppressed ovarian weight. Females irradiated on 11-day postnatally were most adversely affected by radiation, exhibiting a low ovarian weight, and the least mean number of corpus lutea and follicles. Curvey[6] found that irradiation on days 6 and 8 of postnatal life resulted in decreased fertility and females irradiated 11- and 15-day postnatally were almost completely sterile. The data on ovarian weight and number of corpus lutea and follicles obtained are in close agreement with the reduced fertility.

Periods of approximately equal maximum sensitivity are observed in both male and female hamsters, but this period is approximately 10 days later in females than in males[5]. A similar relationship was also noted in rats[13], but in the rats, maximum sensitivity in the male occurred during prenatal life while it occurred during postnatal life in the female. Possible reasons for the differences between sexes will be explored in relation to the patterns of gonad development.

The study of development of ovaries of fetal and neonatal hamsters did not reveal marked changes in morphology of the germinal elements. The normal hamster ovary at day 13 of prenatal life did not show any internal organization, but somatic and germinal elements were distinguishable microscopically. Meiosis was initiated at day 15 of prenatal life while the organization of sex cords appeared to begin. Mitotic activity was observed during days 1 and 3 of postnatal life. Mitosis was discontinued and the ovigenous cords were disrupted. "Nests" of several oocytes formed at day 7 of postnatal life. Primordial and growing follicles were present from day 10 of postnatal life on. The above observations are similar to what Erickson[7] found in the prenatal bovine ovary.

The initial period of sensitivity at day 15 of prenatal life was associated with the preliminary organization of the ovary into sex cords and relatively high mitotic activity. The stage of development appears to be similar to that of rats at day 15 of prenatal life during which Beaumont[2,3] observed increased radiosensitivity. However, high mitotic activity which Beaumont associated with peak radiosensitivity was observed in the hamster at day 1 of postnatal life, a period at which the hamster ovary was more radioresistant.

The second period of high ovarian sensitivity on days 11 and 15 of postnatal life was associated with the completion of organization of follicular cells around all of the oocytes, the appearance of rapidly growing follicles, and also a rapid increase in the total size of the ovary. However the morphology of the oocytes themselves appeared to be similar in stages preceding and following the period of highest sensitivity.

Radiosensitive day 11 of prenatal life coincided with peak mitotic activity of oogonia and radiosensitive days 11 and 15 of postnatal life are the stage at which follicles began to grow. The pattern of ovarian radiosensitivity described here for the hamster is similar to that reported for other mammals. Beaumont[3] reported the inference that the phase of high radiosensitivity coincides with peak mitotic activity of oogonia and that sensitivity declines as the germ cells enter the prophase of meiosis is fully substantiated by her study of rats. It has long been known that primordial oocytes in the rat and mouse are highly susceptible to cell death induced by radiation and disappear within a short time. Cells at a comparable stage of development in the prepubertal and mature rhesus monkey are extremely radioresistant. The higher radioresistance of the monkey ovary, Baker and Beaumont[1] concluded, may be in part because the phases of gamatogenesis are not synchronized. They also found that oocytes which become organized as primordial follicles, seem more susceptible to radiation damage at the time of birth than at later stages. Early primordial oocytes represent the most radiosensitive phase in gametogenesis. Differences in the radiation response may be correlated with variations in nuclear morphology. The susceptibility of cells to radiation induced cell death and mitotic inhibition is known to vary in phase with different stages of the cell cycle, and may be correlated with metabolic activity.

Observations of the irradiated ovaries have been compared with those made in the study of normal gonadal development. The present results indicate that there is a relationship between the quantitative and qualitative changes in the gonads with increasing age and radiosensitivity.

In histological analysis of ovaries, recognizing the early stages of primordial follicles and late stages of primordial follicles and late stages of corpus lutea was difficult. Difficulty was also encountered in choosing typical or representative ovarian sections, a vesicular follicle on one section does not always look like the vesicular follicle on the sections preceeding or following it. Thus improvements in the technique of classifying follicles should be worked out.

A study on developing ovaries of hamsters at every day during the period of rapid development instead of every few days would give a more complete picture of the process of development. Additional quantitative and qualitative analysis could provide a more thorough description of the process of gonadal development in the hamster.

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雌性 Golden Hamsters 之性腺發展及其與放射線照射之關係

雌性 Golden Hamsters 爲本試驗之材料，在其胚胎期第 13 與 15 天及新生期第 1、3、6、8、11、15、與 22 天以 220R 之 X 光照射之。照射組及對照組各取十隻於第 50 天時予以解剖並加以分析。

結果各照射組之卵巢重量平均值都大大降低，其中受影響最大的是胚胎期第 13、15 兩天及新生期第 11 天照射的三組，受影響最少的是第 22天照射的一組。以卵巢中濾泡及黃體總數之減少程度爲指標指出易受放射線影響之時期，則其一在胚胎期第 15 天，另一易感期在新生期第 8、11 及 15 天；而最易於受照射影響的是在第 11 天照射的一組，此雄性遲了十天。至於卵巢重量與濾泡及黃體之總數並無太大的正相關 ($r=0.30$)。照射組除胚胎期第 13 天者，其生長性濾泡均少於對照組；就始基卵泡言，亦以對照組爲最多；黃體則以新生期第 1 及 8 天照射之二組爲數較多。受精力試驗結果尚能符合。

由胚胎期及新生期性腺之正常發展作分析而得知，雌性之最高易感期與下述各項情形，即卵原細胞周圍的濾泡細胞正完成其組織之形成，快速生長性之濾泡出現，以及整個卵巢體積之迅速增加同時發生。然而卵原細胞本身在此最高易感期前後，其形態上並未有任何特別的改變。