

Sexual Segregation in the Left and Right Horns of the Gerbil Uterus: "The Male Embryo is Usually on the Right, the Female on the Left" (Hippocrates)

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We examined reproductive tracts of 253 female Mongolian gerbils (*Meriones unguiculatus*) and recorded the uterine locations (relative to siblings of opposite sex) in which 812 male and 823 female fetuses were found. Within-litter comparisons revealed that sexes were not distributed randomly across uterine horns. The percentage of males in right horns (55.0%) was greater than the percentage of males in left horns (41.8%) and the percentage of females in right horns (45.0%) was significantly less than the percentage of females (58.2%) in left horns. We did not find differences in the total number of fetuses in left and right uterine horns or a sex bias in the total sample of 1635 fetuses. Results were discussed in terms of: (a) effects of sexual segregation of fetuses on expected probabilities of fetuses developing adjacent to 0, 1, or 2 fetuses of opposite sex and (b) consequent alterations in expected frequencies of behavioral phenotypes in populations of gerbils.

The uterine locations of male and female fetuses, relative to fetuses of the same or opposite sex, are associated with important differences in the physiological, morphological, and behavioral characteristics of adult members of all litter-bearing rodent species (mice, rats, hamsters, and gerbils) that have been examined to date (Clark & Galef, 1988; Clemens, 1974; Clemens, Gladue, & Coniglio, 1978; vom Saal, 1981, 1989a; vom Saal & Bronson, 1978; Vomachka & Lisk, 1986). For example, female house mice (*Mus musculus*) that, as fetuses, developed between two males achieve puberty at a later age (Gandelman, vom Saal, & Reinisch, 1977;

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McDermott, Gandelman, & Reinisch, 1978; vom Saal, 1981, 1989b), have longer estrous cycles (vom Saal & Bronson, 1980b; vom Saal, Pryor, & Bronson, 1981), are less fecund (vom Saal & Moyer, 1985), and are both more aggressive towards and less sexually attractive to males (vom Saal & Bronson, 1978, 1980a) than are female mice developing adjacent to no males. Male mice that reside *in utero* adjacent to no male fetuses have lower body weights (Kinsley et al., 1986), and are both less aggressive toward males and less parental towards offspring than are males developing in other uterine locations (Svare, Kinsley, Mann, & Broida, 1984; vom Saal, 1983).

Parallel effects of uterine position on phenotype, generally of greater magnitude than those observed in house mice, have also been found in Mongolian gerbils (*Meriones unguiculatus*), the subject species in the present study. For example, female gerbils that as fetuses occupied uterine locations adjacent to either one or two males, as adults, exhibited enhanced aggression, delayed puberty, reduced litter size, and only half the lifetime fecundity of females that matured in uterine locations distant from males (Clark & Galef, 1988; Clark, Spencer, & Galef, 1986a, 1986b).

The probability of an individual fetus of either sex developing adjacent to 0, 1, or 2 fetuses of the opposite sex depends on four variables: (a) the sex ratio and (b) the size of the litter of which the fetus is a member, and the distribution both (c) within and (d) between uterine horns of male and female siblings. Consequently, each of these four variables is an important developmental determinant of the relative frequencies of the behavioral phenotypes to be found in adult populations both of gerbils and of other litter-bearing rodents.

Vom Saal (1981) has examined the position of male and female mouse fetuses within individual uterine horns and found no significant variation from a random distribution. Below, we focus on the distribution between uterine horns of male and female gerbil fetuses and the consequences of that distribution for uterine exposure to siblings of opposite sex.

Review of the literature reveals a number of asymmetries between mammalian uterine horns, with the right horn exhibiting higher ovulation rates, greater numbers of implantation sites, and higher survival rates of embryos than the left (Asdell, 1964; Baird & Birney, 1985; Barr, Jensch, & Brent, 1970; Buchanan, 1974; Falconer, Edwards, Fowler, & Roberts, 1961; McLaren, 1963; O & Chow, 1987; Stotsenburg, 1915; Weir, Haubenstock, & Beck, 1958; Wimsatt, 1975, 1979). We have, however, found no reference to sexual segregation between uterine horns since Hippocrates (1959, p. 171) proposed, in the fifth century B.C., "that the male embryo is usually on the right, the female on the left." In the present study, we examined the uterine positions of male and female Mongolian gerbil fetuses to determine whether the sexes were randomly distributed between left and right uterine horns.

Methods

At 90 days of age, 253 nulliparous female Mongolian gerbils (*Meriones unguiculatus*), born to breeding stock acquired from Tumblebrook Farms (Brookfield, MA) and reared in the McMaster colony, were each placed with a proven male. Breeding pairs were housed individually in polypropylene cages (35 × 30 × 15 cm), which were lidded with hardware cloth, carpeted with a thin layer of

wood-chip bedding (Beta Chip, Northeastern Products, Warrensburg, NY), and maintained in a temperature-controlled colony room, illuminated on a 12/12 hr light-dark cycle.

The day on which a pair mated was determined using time-lapse video recording and the pair was separated within 12 hr of copulation, with the expectation that a female would give birth 25 days following a copulatory episode. Twenty-four days following observed copulation, each female that had gained weight at a rate consistent with her impregnation on the day of copulation was anesthetized by ether inhalation, her uterus was externalized, and her pups were removed singly. The position and gender of each fetus in left and right uterine horns was recorded. The dam was then euthanized. After participating in the present study, the 1635 pups that we Caesarian-delivered from our 253 subject dams went on to serve in a number of further experiments, to be reported elsewhere.

Gender of pups was determined on the basis of ano-genital distance (Raible & Gorzalka, 1987). Accuracy of prenatal gender determination was verified for 543 offspring in 83 of the 253 Caesarean-delivered litters. Pups in these 83 litters were toe-clipped at delivery for permanent identification. Each of the 83 litters was then fostered-reared by a female that had vaginally delivered a litter on the day of Caesarean delivery of her foster pups. The gender of all individually-marked, foster-reared, Caesarean-delivered pups was reestablished at 45 days of age, when pup gender is absolutely unambiguous even to a first-time observer of gerbils.

Data Analysis

To determine whether male and female fetuses were randomly distributed between left and right uterine horns, we (a) compared the sex ratio in the left uterine horn with the sex ratio in the right uterine horn of each dam, (b) compared the number of male and female fetuses in the left horn with the number of male and female fetuses in the right uterine horn of each dam, and (c) calculated a distribution of differences in the number of male and female fetuses found in the left and right uterine horns of individual dams.

We analyzed the same data three different ways because there was no obvious best analysis, and failure to find significant effects using any one of the three types of analysis we employed would have cast doubt on the validity of any significant effects we found in the other two analyses.

Results and Discussion

Percentage of Males and Females in Left and Right Uterine Horns

If there were a non-random distribution of male and female fetuses in left and right uterine horns of female gerbils, one would expect to find both (a) a greater percentage of males in one uterine horn than in the other and (b) a greater percentage of females in the horn having a lower percentage of males than in the horn having a greater percentage of males.

The 253 dams in the present study were delivered of 1635 live fetuses; 805 fetuses were found in the left uterine horn and 830 in the right. Data describing the mean percentage of males/litter in left and right uterine horns for litters of 1 to 10 pups are presented in Table 1.

Table 1
Mean Percentage of Male Fetuses and Mean Number of Fetuses of Both Sexes in the Left and Right Uterine Horns of Gerbil Dams

Litter size	Number of litters	Mean Percentage of Males ^a		Mean Number of Fetuses	
		Left horn	Right horn	Left horn	Right horn
1	3	0	33.3 ± 33.3	0.7 ± 0.3	0.3 ± 0.3
2	2	0	50.0 ± 50.0	1.5 ± 0.5	0.5 ± 0.5
3	9	42.2 ± 15.5	53.7 ± 14.4	1.1 ± 0.4	1.9 ± 0.4
4	17	44.1 ± 10.4	70.1 ± 8.1	1.8 ± 0.3	2.2 ± 0.3
5	34	35.4 ± 5.1	52.2 ± 6.9	2.7 ± 0.2	2.3 ± 0.2
6	52	41.5 ± 5.0	54.2 ± 4.1	2.6 ± 0.2	3.4 ± 0.2
7	72	45.7 ± 3.1	54.4 ± 3.4	3.6 ± 0.1	3.4 ± 0.1
8	37	43.9 ± 4.0	53.2 ± 4.1	4.1 ± 0.2	3.9 ± 0.2
9	20	44.4 ± 4.6	54.4 ± 6.4	4.5 ± 0.2	4.6 ± 0.2
10	7	35.3 ± 8.0	62.8 ± 10.5	4.4 ± 0.4	5.6 ± 0.4
Total sample	253	41.8 ± 2.0	55.0 ± 2.0	3.3 ± 0.1	3.2 ± 0.1

^a Mean percentage of females in a uterine horn can be calculated by subtracting the mean percentage of males in that horn from 100.

As can be seen from examination of the data presented in Table 1, the sexes were not randomly distributed between uterine horns. Segregation of fetuses by sex in the two uterine horns was indicated by the findings that (a) in litters of each size from 1 to 10, the mean percentage of males in the right uterine horn was greater than the mean percentage of males in the left uterine horn (Wilcoxon matched-pairs signed-rank test, $t = 0$, $p < .01$); (b) in all litter sizes from 1 to 10, the mean percentage of males in the left uterine horn was less than 50% (Sign test, $p < .002$); and (c) the mean percentage of males in the right uterine horn was greater than 50% in litters of 3 to 10 pups and less than or equal to 50% only in litters of 1 and 2 pups (Sign test, $p < .04$). As can also be seen in Table 1, summing across all 253 litters, the left uterine horn contained a female-biased sample of pups (mean percentage of males/litter = 41.8 ± 2.0), while the right uterine horn contained a male-biased sample of pups (mean percentage of males/litter = 55.0 ± 2.0 ; correlated t -test, $df = 252$, $t = 4.88$, $p < .0001$).

The sample of 253 litters contained 140 litters in which the percentage of males in the right uterine horn was greater than the percentage of males in the left horn, 86 litters in which the percentage of males in the right horn was less than the percentage of males in the left horn, and 27 litters in which the percentage of males in the right uterine horn equalled the percentage of males in the left uterine horn (Binomial test, $z = 3.52$, $p < .0004$).

Number of Males and Females in Left and Right Uterine Horns

Comparison of the absolute number of males with the absolute number of females resident in left and right uterine horns revealed that of the 253 left uterine

horns examined, 118 contained more females than males, 75 contained fewer females than males, and 60 contained equal numbers of males and females (Binomial test, $z = 2.95$, $p < .003$). On the other hand, of the 253 right uterine horns examined, 117 contained more males than females, 81 contained fewer males than females, and 55 contained equal numbers of males and females (Binomial test, $z = 2.49$, $p < .007$).

Of the 812 male fetuses in the sample, 347 were found in the left uterine horn (mean number of males/horn = 1.37 ± 0.07) and 465 were found in the right uterine horn (Mean number of males/horn = 1.84 ± 0.08 ; correlated t -test, $df = 252$, $t = 4.36$, $p < .001$). Of the 823 female fetuses, 458 were found in the left uterine horn (mean number of females/horn = 1.81 ± 0.07) and 365 in the right uterine horn (mean number of females/horn = 1.44 ± 0.07 ; correlated t -test, $df = 252$, $t = 3.51$, $p < .001$).

Differences in the Distribution of Male and Female Fetuses Between Horns

In order to measure biases in the distribution of male and female pups in the left and right uterine horns of individual dams, we calculated difference scores (a) by subtracting the number of male fetuses in the left uterine horn from the number of male fetuses in the right uterine horn of each dam and (b) by subtracting the number of female fetuses in the left uterine horn from the number of female fetuses in the right uterine horn of each dam. Each dam thus yielded two difference scores, one for male fetuses and one for female fetuses, that were found to range from plus 5 to minus 5. Each of these difference scores was an index of the inequality between the two horns in the number of occupant members of a given sex. If there were no bias in the location of male and female fetuses in the two uterine horns, then one would expect to see no differences between the sexes in the distributions of their respective difference scores.

As can be seen in Figure 1, there were marked differences in the distribution of difference scores for male and female fetuses (Kolmogorov-Smirnov two-sample test, $d = 0.1973$, $p < .001$). Of the 253 litters, there were 122 in which there were more females in the left uterine horn than in the right, 76 litters in which there were more females in the right uterine horn than in the left, and 55 litters in which there were equal numbers of females in the two uterine horns (Binomial test, $z = 3.19$, $p < .0018$). Males were more numerous in the right uterine horn than in the left in 123 litters, more numerous in the left uterine horn than the right in 73 litters, and were equal in number in the two uterine horns in 57 litters (Binomial test, $z = 3.5$, $p < .0004$).

Secondary observations

Some of the substantial asymmetries in the number of male and female fetuses in left and right uterine horns reported above might have been caused by (a) biases in the overall sex ratio of the sample of 1635 fetuses, (b) differences in the total number of fetuses resident in left and right uterine horns, or (c) systematic errors or biases in the attribution of gender to fetuses. However, (a) the sex ratio of the entire sample calculated either as the total number of males to the total number of

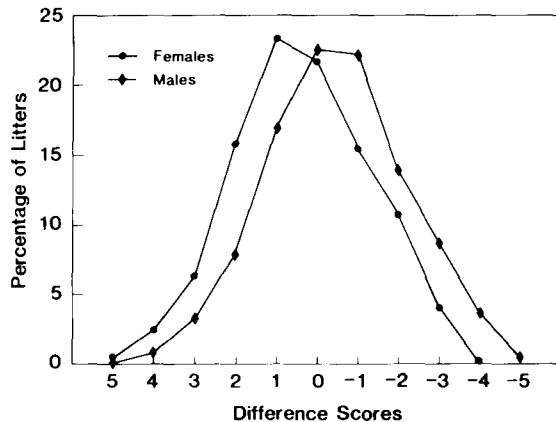


Fig. 1. Distribution of difference scores for male and female gerbils. Difference scores for males were calculated by subtracting the number of male fetuses in the left uterine horn from the number of male fetuses in the right uterine horn of individual dams. Difference scores for females were also calculated by subtracting the number of female fetuses in the left uterine horn from the number of female fetuses in the right uterine horn of individual dams.

females (812/823), as the mean number of males per litter to the mean number of females per litter (3.21/3.25), as the mean percentage of males/litter (49.9 ± 1.3 percent), or as the ratio of predominantly-male litters to predominantly-female litters (103/111 litters) did not deviate significantly from chance; (b) the mean number of fetuses in the left uterine horn (mean = 3.2 ± 0.07 pups/litter) did not differ significantly from the mean number of fetuses in the right uterine horn (mean = 3.3 ± 0.09 pups/litter); and (c) the gender identification at delivery of the 543 pups in the 83 Caesarean-delivered, fostered-reared litters conformed in every instance to gender identification at 45 days of age.

Consequences of Sexual Segregation

Table 2 shows the proportion of male and female gerbil fetuses in left and right uterine horns developing adjacent to 0, 1, or 2 members of the opposite sex. As one would expect on probabilistic grounds alone, other things being equal, given the observed uterine sexual segregation of fetuses, male fetuses in the right uter-

Table 2
The Proportion of Male and Female Gerbil Fetuses in Right and Left Uterine Horns Developing Adjacent to 0, 1, or 2 Siblings of the Opposite Sex

	Male Fetuses			Female Fetuses		
	0	1	2	0	1	2
Uterine Horn:						
Left	.30	.55	.14	.46	.46	.08
Right	.50	.41	.09	.34	.53	.13

ine horn and female fetuses in the left uterine horn were less likely to be located adjacent to 1 or 2 members of the opposite sex than were, respectively, male fetuses in the left uterine horn and female fetuses in the right uterine horn. Appreciation of the magnitude of change in the probability of a fetus being located adjacent to fetuses of the opposite sex resulting from a small change in the intra-uterine distribution of male and female fetuses can be appreciated by considering a specific example. In a litter of 8 fetuses with 2 male and 2 female fetuses in each uterine horn, the *a priori* probabilities of a fetus of either sex being located adjacent to 0, 1, or 2 fetuses of the opposite sex are, respectively, .167, .667, and .167. In a litter of 8 fetuses with 3 male fetuses and 1 female fetus in one uterine horn and 3 female fetuses and 1 male fetus in the other uterine horn (i.e., with the positions of one male and one female reversed), the same expected probabilities are, respectively, .375, .50, and .125. In other words, as a consequence of reversing the uterine horns in which one male and one female fetus were located, the expected probability of an individual of either sex being located adjacent to no members of the opposite sex more than doubled.

It would, of course, be best if we could calculate the impact of sexual segregation of the observed degree on the expected relative frequencies of fetuses developing adjacent to 0, 1, and 2 siblings of the opposite sex. Unfortunately, there is no general solution to the problem of the magnitude of the effect of a particular degree of sexual segregation on the proportion of male and female fetuses developing adjacent to 0, 1, or 2 fetuses of the opposite sex. A unique solution exists for each sample of litters one examines as a function of the distribution of litter sizes, sex ratios, and distributions of pups (irrespective of sex) between horns in that sample.

General Discussion

The results of the present experiment demonstrate an unequivocal bias in the distribution of male and female gerbil fetuses across the uterine horns of their respective dams and a consequent change in the observed probability that male and female fetuses developed adjacent to siblings of the opposite sex. Altering the probability of fetuses developing adjacent to members of the opposite sex would alter the distribution of morphological and behavioral traits in populations of adult gerbils (Clark & Galef, 1988; Clark, Spencer, & Galef, 1986a, 1986b).

Unfortunately, no satisfactory explanation is available in the literature for any of the uterine asymmetries in ovulation or implantation discussed in the introduction to the present paper, and our data provide no insight into the proximate mechanisms responsible for the observed sexual segregation of gerbil fetuses. Selective fertilization of ova by Y-bearing sperm could occur if differences in the structure or morphology of ova released by left and right ovaries affected the probability of Y-bearing sperm penetrating an ovum (Robinson, 1965). Differences in the chemical composition of cervical fluids in the left and right uterine horns could influence the relative longevity of X and Y sperm and their consequent probability of fertilizing an ovum (Shettles, 1970). Differences in uterine conditions might favor differential survival of the sexes, etc. The possibilities are endless. However, migration of blastocytes between uterine horns, an option open to some mammalian species (e.g., pigs, antelope and bats; Asdell 1964; Wimsatt,

1975, 1979), may be unusual in both gerbils and other rodents because the rodent uterus is bicornate, opening into the vagina via two cervixes (Asdell, 1964).

Differential resorption or atrophy of male and female fetuses in left and right uterine horns could have contributed to the asymmetries in distribution of viable male and female fetuses that we observed in Caesarian-delivered litters. Of the 253 litters we examined, 24 contained either atrophied fetuses or resorption sites, and these reproductive failures were more common in the right uterine horn than in the left (Binomial test, $z = 1.88$, $p < .03$). Unfortunately, it was not possible to determine the gender of failed fetuses, so we could not estimate the contribution of gender differences in fetal loss in each uterine horn to gender differences in the distribution of viable fetuses. However, no atrophied fetus or resorption site was observed in any of the 64 litters containing 8, 9, or 10 pups, and these large litters exhibited sex biases in uterine distribution of fetuses similar to those seen in the 189 smaller litters we examined (see Table 1). Hence, differential loss of male and female fetuses in right and left uterine horns could not be the sole cause of the sex bias in uterine location reported here.

Regardless of the mechanisms underlying the observed sexual segregation of fetuses in the uterine horns of Mongolian gerbils, the alterations in probabilities of gerbil fetuses developing adjacent to siblings of the opposite sex resulting from uterine sexual segregation must have pronounced effects on observed frequencies of behavioral phenotypes in populations of adult Mongolian gerbils. Other things being equal, sexual segregation of gerbil fetuses in left and right uterine horns must result in greater numbers of fetally-masculinized adult male gerbils and smaller numbers of fetally-masculinized adult female gerbils than one would otherwise observe.

Notes

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