Seasonal variations in the response of the testis and LH levels to hemicastration of adult rams

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Summary. The weight and histology of the testis and plasma LH levels were analysed after hemicastration of adult Ile-de-France rams in spring or in autumn. After hemicastration, the remaining testes were significantly heavier than those of entire animals measured at the same time of year. At 4 or 6 months after hemicastration performed in spring, the remaining testes were hypertrophied by nearly 40% as compared to the testes of entire sexually active animals, assessed in autumn. The variations of intertubular tissue volume, total seminiferous tubule length, stem cell stocks, daily production of round spermatids, and cellular volume of primary spermatocytes paralleled the variations in testis weight. The annual decrease of the area of the Sertoli cell nuclei and of the yield of meiosis and beginning of spermiogenesis during the non-breeding season was prevented by hemicastration performed in autumn. Plasma LH levels were consistently elevated till autumn after hemicastration performed in spring. A positive and significant correlation was observed between LH levels and yields of spermatogonial divisions.

Introduction

The influence of unilateral orchidectomy on the remaining testis has been studied in the adult ram by several investigators. Some reported features of the compensatory hypertrophy after hemicastration were an enlargement of the remaining testis and epididymis (Voglmayr & Mattner, 1968; Renfro & Dutt, 1970; Skinner, 1971; Johnson, Desjardins & Ewing, 1971) and an increase in the epididymal sperm reserve (Voglmayr & Mattner, 1968). Further, testicular protein and steroid synthesis were stimulated (Johnson *et al.*, 1971) and plasma testosterone (Johnson *et al.*, 1971) and LH (Hochereau-de Reviers & Pelletier, 1971) levels were increased. In these experiments, however, no account of the influence of season was taken, although it is known that the ram is a seasonal breeder.

The object of the present experiment was to analyse the effect of hemicastration in spring and in autumn on ten testicular parameters in Ile-de-France rams. The influence of hemicastration on plasma LH levels was also investigated.

Materials and Methods

Adult Ile-de-France rams were maintained under natural seasonal variations in daylength. Two groups of rams were used. In each group the first testis removed from every animal was labelled E (entire) and the second C (castrated). In the first group, rams were hemicastrated randomly throughout the year (Group 1E; N = 48) and the second testis was removed 4 months later (Group 1C; N = 27). In this group, only rams which were hemicastrated in March–April or in September–October were used for the analysis of cellular volume of germ cells. In the second group, rams were hemicastrated either in March at the beginning of spring (Group 2ES; N = 9) or in October at the beginning of autumn (Group 2EA; N = 9). Complete castration was carried out after a delay of 6 months, i.e. in autumn (Group 2CA; N = 9) and in spring (Group 2CS; N = 3).

After removal the testes were weighed, and fragments of each testis from rams in Group 2 were fixed and analysed as previously described (Hochereau, 1967). The relative volumes of intertubular tissues and seminiferous tubules were determined with a 25-point ocular integrator (I Zeiss: Hennig, 1957), on 40 fields for each testis. The total volumes of intertubular and tubular tissue were then calculated. The diameters of the tubules were measured with an ocular micrometer on 20 cross-sections of tubules/testis. The total length of seminiferous tubule/testis was calculated from the above data by the formula of Attal & Courot (1963).

The stages of the cycle of the seminiferous epithelium were classified as described by Ortavant (1958). Type A₀ and A₁ spermatogonia (Hochereau-de Reviers, Ortavant & Courot, 1975) were counted in 10-µm thick cross-sections of 10 tubules at stages 6–7, 8 and 1 respectively. Primary spermatocytes at leptotene and round spermatids were counted in 10 tubular cross-sections at stages 2 and 1, respectively. The true numbers of these cells per cross-section were calculated by the formula of Abercrombie (1946) as modified by Ortavant (1958). Total numbers of type A₀ and A₁ spermatogonia/testis were calculated from the total length of seminiferous tubules and the mean corrected number of A₀ and A₁ spermatogonia/10 µm tubular cross-section.

The yield of spermatogonial divisions was calculated from the number of primary spermatocytes at leptotene divided by the number of type A₁ spermatogonia. The daily production of round spermatids/testis was calculated as described by Ortavant (1958). The area of the nuclei of Sertoli cells, type A₀ and A₁ spermatogonia (at stages 6 to 1), primary spermatocytes at leptotene (stage 2), and round spermatids (stage 1) were estimated from camera lucida drawings. Twenty nuclei/cell type were analysed.

Primary spermatocytes and round spermatids were separated by velocity sedimentation at unit gravity and sedimentation velocities, and mean cell volumes were determined with a Coulter Counter by the method of Loir & Lanneau (1974). The theoretical relationship, $\log V = K + 3/2 \log S$, between cell volume, V , and sedimentation velocity, S , was verified with the present material.

Blood was withdrawn from 10 intact and 10 hemicastrated animals by acute puncture of the jugular vein. The sampling took place on the morning and the afternoon of the 2 days before the hemicastration, then twice a month from March to September. Plasma samples were kept frozen until assayed by a specific radioimmunoassay (Pelletier, Kann, Dolais & Rosselin, 1968). The results are expressed as ng LH-M3, a purified ovine hormone whose activity is $\times 1.8$ the NIH-LH-S1 standard.

Table 1. The effect of hemicastration on the adult ram testis

	Season					
	Spring			Autumn		
	Group 2ES	Group 2CS	% change	Group 2EA	Group 2CA	% change
Testis weight (g)	182 ± 24	240 ± 9	+32	247 ± 12	356 ± 23	+44
Intertubular tissue volume (cm ³)	33.4 ± 3.7	40.4 ± 3.6	+21	51.6 ± 3.4	73.1 ± 4.3	+41
Length of seminiferous tubules/testis (m)	2574 ± 276	3055 ± 110	+19	3714 ± 322	4695 ± 310	+27
Diameter of seminiferous tubules (µm)	219 ± 7	238 ± 10	+9	219 ± 8	224 ± 6	+2
Type A ₀ spermatogonia/testis ($\times 10^6$)	252 ± 50	515 ± 120	+104	530 ± 161	775 ± 108	+46
Type A ₁ spermatogonia/testis ($\times 10^6$)	343 ± 34	572 ± 56	+67	558 ± 60	781 ± 82	+40
Spermatocytes I (leptotene)/A ₁ spermatogonia	19.5 ± 2.2	17.9 ± 1.2	−10	26.3 ± 1.8	28.5 ± 2.0	+8
Round spermatids/spermatocytes I (leptotene)	2.8 ± 0.2	3.4 ± 0.3	+21	3.0 ± 0.1	2.8 ± 0.1	−8
Round spermatids production/testis/day (10^9)	1.9 ± 0.3	3.3 ± 0.3	+70	3.9 ± 0.3	5.7 ± 0.5	+46

Values are Means ± S.E.M.; see text for numbers of animals and details of groups.

Results

Effects of season in intact animals

The results are shown in Tables 1, 2, 3 and 4 and Text-fig. 1.

Testis. The testis weight, the volume of intertubular tissue and the total seminiferous tubule length/testis increased significantly by 40%, 55% and 50%, respectively, between spring and autumn.

There was no significant variation of tubular diameter (Tables 1 and 2).

Table 2. Factorial analysis of variance of the differences between parameters measured in normal or hemicastrated testes, removed in spring or in autumn from Ile-de-France rams

Parameter	Season	Hemicastration	Interaction
Testis weight	$P < 0.001$ $F = 13.0$	$P < 0.001$ $F = 16.2$	N.S.
Intertubular tissue vol.	$P < 0.001$ $F = 28.4$	$P < 0.001$ $F = 15.0$	N.S.
Length of seminiferous tubules/testis	$P < 0.001$ $F = 15.0$	$0.01 < P < 0.05$ $F = 5.8$	N.S.
Diam. of seminiferous tubules	N.S.	N.S.	N.S.
Total no. type A ₀ spermatogonia/testis	$P = 0.05$ $F = 4.3$	$0.01 < P < 0.05$ $F = 3.7$	N.S.
Total no. type A ₁ spermatogonia/testis	$P < 0.01$ $F = 9.4$	$P < 0.01$ $F = 10.6$	N.S.
Yield of spermatogonial divisions	$P < 0.001$ $F = 13.1$	N.S.	N.S.
Yield of meiosis and beginning of spermiogenesis	N.S.	N.S.	$P < 0.01$ $F = 8.1$
Daily production of round spermatids/testis	$P < 0.001$ $F = 26.0$	$P < 0.001$ $F = 15.2$	N.S.

Sertoli and germ cells. The size of Sertoli cell nuclei increased by nearly 20%, and total numbers of type A₀ and A₁ spermatogonia/testis increased by 100% and 60%, respectively. The yield of spermatogonial divisions varied significantly by 35% but that of meiosis and the beginning of spermiogenesis was only slightly increased.

Text-fig. 1. Annual variation of the weight of the remaining testis, 4 (Group 1C, ●) or 6 (Group 2CA(Δ) and Group 2CS(▲)) months after hemicastration of Ile-de-France rams, expressed as a % of the weight of the testis.

There was a 100% increase of the daily production of round spermatids/testis, but the nuclear size of A₀ and A₁ spermatogonia, of leptotene primary spermatocytes and of round spermatids diminished slightly.

The cellular volume of pachytene spermatocytes and round spermatids increased significantly by 8% and 12% respectively between the non-breeding and the breeding season.

Table 3. Mean ($\pm$ S.E.M.) nuclear size (μm^2) of Sertoli and germ cells in the testes of entire (E) or hemicastrated (C) Ile-de-France rams subjected to surgery in spring (S) or in autumn (A)

Cell type	Spring		Autumn	
	Group 2ES	Group 2CS	Group 2EA	Group 2CA
Sertoli cell	47.6 $\pm$ 0.9	63.4 $\pm$ 1.5	56.5 $\pm$ 1.1	57.9 $\pm$ 1.0
A ₀ spermatogonia	42.6 $\pm$ 0.7	41.7 $\pm$ 1.2	39.8 $\pm$ 0.6	39.6 $\pm$ 0.6
A ₁ spermatogonia	50.2 $\pm$ 1.0	52.3 $\pm$ 1.7	50.6 $\pm$ 0.8	50.5 $\pm$ 0.8
Leptotene I spermatocytes	30.6 $\pm$ 0.4	32.8 $\pm$ 0.6	29.6 $\pm$ 0.3	31.9 $\pm$ 0.4
Round spermatids	18.8 $\pm$ 0.3	18.7 $\pm$ 0.4	17.5 $\pm$ 0.2	19.4 $\pm$ 0.3

Summary of analysis of variance for Sertoli cell nuclei:

2ES versus 2EA, $F = 8.7$; d.f. 16, 1; $0.001 < P < 0.01$.

2ES versus 2CA, $F = 12.2$; d.f. 16, 1; $P < 0.001$.

2ES versus 2CS, $F = 15$; d.f. 10, 1; $P < 0.001$.

Effect of hemicastration

The results are shown in Tables 1, 2, 3 and 4 and Text-fig. 2.

Testis. The effect of hemicastration on testis weight, intertubular tissue volume and total length of seminiferous tubules/testis was greater in autumn than in spring (Table 1). The diameter of the seminiferous tubules was not affected by hemicastration (Tables 1 and 2).

Table 4. Mean ($\pm$ S.E.M.) cellular size (μm^3) of primary spermatocytes at pachytene and round spermatids in the testes of entire (1E) or hemicastrated (1C) Ile-de-France ram subjected to surgery in spring or in autumn

Cell type	Spring		Autumn	
	Group 1ES (N = 25)	Group 1CS (N = 3)	Group 1EA (N = 18)	Group 1CA (N = 11)
Pachytene I spermatocytes	2336 $\pm$ 144	2428 $\pm$ 295	2517 $\pm$ 106	2507 $\pm$ 238
Round spermatids	694 $\pm$ 34		780 $\pm$ 30	

For Group 1ES versus Group 1EA: $F = 59.98$; $P < 0.001$.

For Group 1CS versus Group 1ES: $F = 3.90$; N.S.

Sertoli and germ cells. The total numbers of A₀ and A₁ spermatogonia/testis and the daily production of round spermatids/testis increased more after hemicastration in spring than in autumn. The yield of spermatogonial divisions was not affected. Ablation of one testis increased the yield of meiosis and beginning of spermiogenesis, and the nuclear size of Sertoli cells only in the remaining testis of spring animals. Similarly, the cellular volume of pachytene I spermatocytes was elevated slightly but nonsignificantly, in animals hemicastrated in spring.

Plasma LH levels. The concentrations of LH in samples collected in the morning did not differ significantly from those of samples collected in the afternoon in either entire or hemicastrated rams. Consequently, the two values were pooled (Text-fig. 2). The LH levels of the two groups were similar before hemicastration. Following surgery, the LH levels in the hemicastrated animals were consistently higher than that of control animals over the 6-month period of bleeding; analysis of variance indicated that this difference was significant ($P < 0.01$).

Text-fig. 2. Plasma LH levels in hemicastrated Ile-de-France rams (○) and in control animals (●) over a 6-month period between spring and autumn.

Discussion

Hemicastration in spring induces a true hypertrophy of testis weight in the adult Ile-de-France ram. When the removal of the first testis occurs in autumn the weight of the remaining testis is maintained so that the autumn hemicastration appears to counteract the normal seasonal decrease. If the animals are left for a year, the remaining testis taken in spring or in autumn is equivalent to that of a hemigonadectomized animal castrated 6 months later (unpublished data), indicating that animals hemicastrated in autumn can only develop true hypertrophy after a delay of 6 months.

These data agree with previous results obtained in the ram (Voglmayr & Mattner, 1968; Hochereau-de Reviers & Pelletier, 1971; Skinner, 1971; Johnson *et al.*, 1971). However, some interbreed differences may occur. For example, in the Préalpes breed, which shows small seasonal variations of testis weight, a true hypertrophy is observed throughout the year (M. Loir, unpublished data).

Compensatory hypertrophy has been observed in a number of adult seasonal breeders (rabbit: Ribbert, 1890; badger: Canivenc & Relexans, 1967; field vole: Delost, 1972; Martinet & Meunier, 1975), but only in the nonpubertal or prepubertal rat or bull (Hochereau-de Reviers, 1970, 1971). This fact could be related to the absence of annual variation in sexual activity in these animals.

The increase in testis weight after hemicastration or during seasonal variation appears to be due both to the intertubular tissue and to the seminiferous tubules. Compensatory hypertrophy of the intertubular tissue has been observed in rabbits and guinea-pigs by Ancel & Bouin (1903), and in rats by San Filippo (1970). The intertubular tissue increases in the ram after hemicastration during spring, but hemicastration in autumn does not completely counteract the intertubular regression. The development of the intertubular tissue after hemicastration suggests an increase of testosterone release by the remaining testis (Johnson *et al.*, 1971). The testosterone increase could be modulated photoperiodically since variations in plasma testosterone levels throughout the year in the intact ram have been shown by Attal (1970), Johnson *et al.* (1973), Katongole, Naftolin & Short (1974), and Sanford, Palmer & Howland (1974).

In the present experiment, the effect of season or hemicastration on seminiferous tubules is evident on the tubule length but not on the diameter. In another study on more animals of the same breed, however, a significant variation in tubule diameter has been observed (M. T. Hochereau-de Reviers & M. Loir, unpublished) between spring (189 ± 4 (S.E.) μm) and autumn (216 ± 4 μm). Moreover, in a previous experiment on the action of hemicastration, tubule diameter increased as early as 1 month after hemicastration during spring, and was equal to the autumnal value in June. In autumn, the diameter decrease was prevented by hemicastration (Hochereau-de Reviers & Pelletier, 1971). The present negative results could have been due to the high within-group variance for this criterion.

The total number of spermatogonia is assumed not to vary in the adult, but this should only be true for mammals that are sexually active throughout the year. The total number of A_0 spermatogonia/testis, the reserve stem spermatogonia according to Clermont (1967), doubled between spring and autumn. Hemicastration always increased these numbers. This was not significant because of the great heterogeneity of the two groups (2 ES versus 2 EA). The total number of A_1 spermatogonia/testis, the renewing stem spermatogonia according to Clermont (1967), increased significantly between spring and autumn and was augmented after hemicastration at both seasons. A 10% increase in A_1 spermatogonia/tubular cross-section in Ile-de-France rams between spring and autumn has been reported by Ortavant (1959).

The yield of spermatogonial divisions increases in the sexually active ram (Ortavant, 1958). The results of the present study indicate that hemicastration does not lead to further increase. In an earlier experiment we observed that, after hemicastration in March, the yield of spermatogonial divisions had increased after only 1 month, whereas in the ram hemicastrated in autumn it decreased more slowly (Hochereau-de Reviers & Pelletier, 1971). Finally, hemicastration partly delays the seasonal reduction of that yield and the increase during spring is advanced.

Although only small differences between the values of the yield of meiosis and the beginning of spermiogenesis in spring and autumn were observed in our animals, significant variations of these processes throughout the year have been clearly demonstrated by Ortavant (1958). Hemicastration performed in autumn appears to eliminate the decrease during the non-breeding season (Groups CS and ES). This could be related to the increase in activity of Sertoli cells indicated by increase in the area of their nuclei. Similar variations of Sertoli cell nuclei were observed by Vendrely, Guerillot & Da Lage (1972) in the hamster testis.

The area of the germ cell nuclei does not vary significantly with seasons or after hemicastration, but the method of analysis was possibly not precise enough to show small variations. Seasonal variations of primary spermatocytes and round spermatid cell volumes did occur; the effect of hemicastration was not significant but it seemed to eliminate their decrease during the non-breeding season.

The present results show that plasma LH increases when rams are hemicastrated in spring. The level is maintained for 6 months over the control values, although in autumn the difference seems to decrease. This result differs from previous observations of rams hemicastrated in autumn in which the plasma LH levels were significantly greater than in controls after 4 days, but were not significantly different after 1 or 2 months (Hochereau-de Reviers & Pelletier, 1971). However, the number in animals and blood samples were fewer than in the present study. Land & Carr (1975) have observed significant increases in plasma LH values in young lambs of various breeds after hemicastration. The increase in testis weight and in the various testicular parameters studied could be related to this spring increase in LH release. Furthermore, the plasma LH level has been found to be positively correlated to the yield of spermatogonial multiplication ($r = +0.49$; $P < 0.05$), although this step in spermatogenesis has been assumed to be independent of gonadotrophin control (Steinberger, 1971).

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