ON THE EFFECTS OF COMPLETE AND INCOM-PLETE CASTRATION UPON HORN GROWTH IN HERDWICK SHEEP. By F. H. A. MARSHALL AND J. HAMMOND.

As has been pointed out in a previous paper, in Herdwick sheep there is a well-marked sexual differentiation, since the rams are horned and the ewes hornless. It was shown further that castration inhibits horn growth forthwith and at any stage of development. In the present paper these results are confirmed and extended.

Effect of complete castration.

The two Herdwick rams (born in May 1910 and May 1911 respectively) and the three Herdwick wethers referred to in the previous paper are still alive. The horns of both the rams are now very well developed, but those of the wethers have undergone no appreciable further growth. The first wether (born in May 1910) still has low, rounded knobs, while the horns of the other two (born in May 1911) are about $4\frac{1}{4}$ and 6 inches long respectively, these being their lengths at the time of castration.

Two more ram lambs, born in May 1912, were castrated in the following September, the testes and epididymes being completely removed. On the day of the operation their horns were measured, and found to be as follows:—

- (1) Right horn, 5 inches; left horn, 5 inches.
- (2) Right horn, 4½ inches; left horn, 4 inches. Their lengths at present (March 1914) are as follows:—
 - (1) Right horn, 5\frac{3}{8} inches; left horn, 5\frac{1}{2} inches.
 - (2) Right horn, 4½ inches; left horn, 4½ inches.

It is thus seen that the lengths of the horns in the two wethers have not appreciably altered, and the results fully confirm those recorded in the previous paper. The horn lengths should be compared with those of the four animals of the same age described below.

¹ For references, see end of this Paper.

Effect of unilateral castration.

In support of the view that the relation between the gonads and the secondary characters of sex is nervous rather than through the influence of internal secretions it has been alleged that in certain cases of hermaphroditism or of unilateral castration there is a direct correspondence between the sex of the gonad and the secondary characters on the same side of the body as the gonad. Thus Weber has recorded a case of a chaffinch which had a testis on the right side associated with right-sided male plumage and an ovary on the left side associated with left-sided female plumage. This case is quoted by Nussbaum, who regards it as evidence of the influence of the nerves upon the secondary characters of sex. Poll has described three cases of hermaphroditism in which the external characters on each side corresponded





Fig. 1.

The desired Dame and the North March 1011

Fig. 1. Herdwick Ram, normal, born May 1911.
Fig. 2. Herdwick Wether, without horns visible, born May 1910;
castrated August 1910.

with the sex of the gonad on that side. Thus in a bullfinch the gonad and the plumage of the breast on the right side are stated to have been male while those on the left were female. In the case of a pheasant, recently described by Bond, the secondary sexual characters were unilaterally distributed, while there was a single gonad in which the male and female elements were gathered together and lying on the left side but nearer to the middle line than the normal position of the left sex gland.

Among mammals Rörig has described cases of unilaterally castrated stags with abnormal antler development on one side, usually on the opposite side to that on which the testis was absent. Fowler has also

stated that in fallow deer one-sided castration may result in the abnormal or incomplete development of one antler, the other antler being normal.

In our experiments one testis (together with the corresponding epididymis) was removed from each of two Herdwick ram lambs. The lambs were born in May and operated upon in the following September. The following are the records of the experiments:—

(1) September 1913. Right testis removed. Lengths of horns on day of operation, right, $5\frac{1}{4}$ inches, left, 6 inches. Lengths of horns in March 1914, right, $10\frac{1}{2}$ inches, left $10\frac{7}{4}$ inches.





Fig. 3.

Fig. 4.

Fig. 3. Herdwick Wether, born May 1911; castrated October 1911. The horns are the same length as they were at the time of castration.

Fig. 4. Herdwick Ram Lamb, born May 1913; one testis removed September 1913.

The horns have continued to grow and are symmetrical.







Fig. 6.

Fig. 5. Herdwick Wether, born May 1913; castrated September 1913.
Fig. 6. Herdwick Wether, born May 1913. The testes were removed in September 1913 but the epididymes retained.

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(2) September 1913. Left testis removed. Lengths of horns on day of operation, right, $4\frac{1}{2}$ inches, left, $4\frac{1}{8}$ inches. Lengths of horns in March 1914, right, $8\frac{1}{4}$ inches, left, $8\frac{1}{2}$ inches.

It is thus seen that the removal of one testis only had no effect upon the symmetry of the horns. It is also seen that one testis only was able to supply sufficient stimulus to permit of the continuance of the horn growth. It is to be remarked, however, that the horn growth was much slower than that of the normal rams previously described. In one of these each of the horns was already eleven inches long in December when it was only seven months old. Possibly however there may be considerable variation in the rate of horn growth in normal Herdwick rams.

Effect of removing the testis but retaining the epididymis.

It has been suggested that the epididymis may exert a controlling influence on the development of the secondary male characters (Biedl), but so far as the authors are aware there is no actual evidence that this is the case. It seemed desirable, however, that the matter should be put to the test in Herdwick rams by removing the testis on each side but leaving the epididymis in position. This was accordingly done in the case of two male Herdwick lambs which were born in May and operated upon in September. The following are the records of the horn lengths on the day of the operation and at the present time:—

- (1) September, right horn, $5\frac{1}{2}$ inches, left horn, $6\frac{1}{4}$ inches. March, right horn, 6 inches, left horn, $6\frac{1}{4}$ inches.
- (2) September, right horn, $2\frac{3}{4}$ inches, left horn, $2\frac{7}{8}$ inches. March, right horn, $3\frac{1}{8}$ inches, left horn, $3\frac{1}{4}$ inches.

It is thus seen that there was practically no further horn growth after castration, and thus, that the removal of the testes alone without the epididymes was sufficient to inhibit such growth. The epididymes in the two wethers can still easily be felt in the scrotal sacs.

Discussion.

Geoffrey Smith as an alternative to the hormone hypothesis regarding the relation between the gonads and the secondary sexual characters has put forward another theory which he calls the theory of metabolic stimulation. According to Smith's view "the gonad, by feeding on certain specific substances in the blood, stimulates the overproduction of these substances by the metabolic organs, and so brings

about changes in the composition of the blood, which act as a stimulus on the secondary sexual characters." This theory in another paper is fully elaborated for certain Crustaceans, in terms of fat metabolism, but Smith is careful to state that he regards the changes in the fat content of the blood which this theory postulates (and for which there is actual evidence based on estimation experiments) as merely an accompaniment of more deep-seated changes. It is an essential part of Smith's theory that fat molecules together with "fat-links" are given off from the liver and carried to the gonad which absorbs the molecules but releases the links. The latter are supposed to pass back to the liver and to fix on to new fat molecules which are borne to the gonad as before. This continued process is believed to lead to the regeneration of new fat-chains in the liver, and the result of the whole series of changes is to flood the blood with a large number of fat-link and fat combinations and of free fat-links. These are supposed to stimulate the development of the secondary sexual characters. It is to be observed that since the giving off of free fat-links by the gonad is an essential part of the theory, the gonad on this view is an organ producing an internal secretion which is in some way necessary for the growth of the secondary characters.

The principle underlying Smith's theory is the production in excess of substances which stimulate the development of the secondary sexual characters. This principle is held to be essentially similar to that upon which Ehrlich's side-chain theory of immunity is based. But according to the immunity theory the antibodies with which the blood is flooded remain there for some considerable time after the removal of the exciting cause which was originally responsible for their production. It is clear, therefore, that, on Smith's view, the removal of the testes from Herdwick rams ought to have no result (or at any rate no immediate result) upon the continuance of horn growth, since the specific substances called forth by the gonads would remain in the blood for some considerable time after castration; that is to say, horn growth in Herdwick rams ought to continue after the extirpation of the testes; but this, as has been shown, is not the case.

The results described in this paper clearly support the view that the testes elaborate one or more hormones or internal secretions, which, either directly or indirectly, act as a stimulus to the tissues from which the horns develop. It has not so far been found practicable to attempt to imitate the normal action of this problematical hormone, by injecting fresh extract of ram's testis. It may, however, be pointed out that if

this were done over a considerable period, and the result were negative, this could not be regarded as antagonistic to the hormone theory, since there is really no sound reason for supposing that an emulsion or extract of testicular gland would contain the specific substance or substances unaltered, and in a condition capable of setting on foot the complicated nexus of metabolic processes which results in the development of the secondary characters of sex.

SUMMARY OF RESULTS.

Removal of the testes from Herdwick ram lambs arrests further horn growth forthwith and at any stage of development. Unilateral castration does not stop horn growth, neither does it affect the symmetry of the horns, but there is some evidence that the further development of the horns is slower than in normal unoperated animals. Removal of the testes without the epididymes (these being retained) inhibits horn growth in precisely the same way as ordinary castration in which both organs are removed.

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REFERENCES.

Biedl. "Innere Sekretion," Wien. 1911.

Bond. Journ. of Genetics, III. p. 205. 1914.

Fowler. Proc. Zool. Soc. p. 485. 1894.

Marshall. Proc. Royal Soc. B. LXXXV. p. 27. 1912.

Nussbaum. Ergebn. d. Anat. u. Entwick. xv. p. 39. 1905.

Poll. Stzngsbr. Gesel. Natur. f. Freunde zu Berlin, p. 338. 1909.

Rörig. Arch. f. Entwick.-Mech. viii. pp. 382, 633. 1899. Ibid. x. pp. 525, 618. 1900. Ibid. xi. pp. 65, 225. 1901.

Smith. Linnean Society. March, 1913. Quart. Journ. Micr. Science, Lix. p. 267. 1913.

Weber. Zool. Anz. xIII. p. 508. 1890.