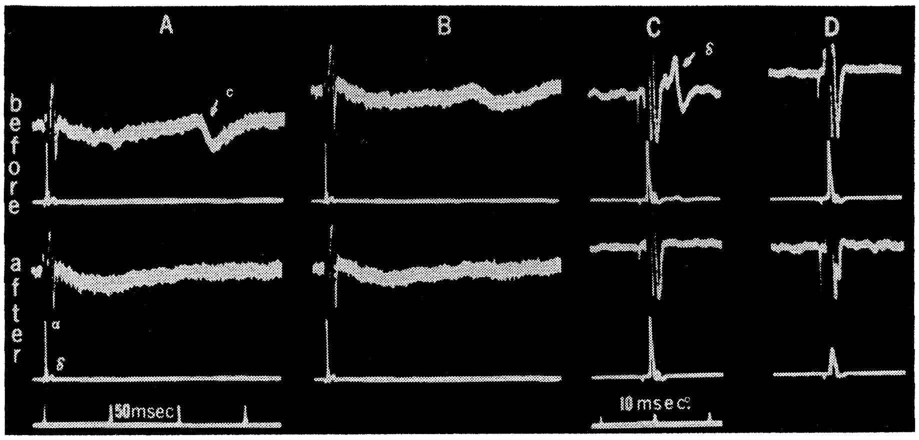

Fig. 1. Oscillographic records of compound action potentials in the saphenous nerve of the cat, showing the effects of irradiation of the nerve with focused ultrasound. The tracings in columns *A* to *D* were photographed at four different times in the course of a series of irradiations. The upper pair of tracings in each column were obtained before, the lower pair after, particular irradiations which blocked conduction differentially. In each pair the upper record is at higher gain. The arrows in columns *A* and *C* indicate the action potentials of C fibers and delta fibers, respectively.

radiation, but there was no alteration in the alpha and delta deflections shown on the lower channel.

The upper pair of action potentials in column *B* were recorded 19 minutes after those in column *A*, and they show recovery of a few C fibers. Twenty additional pulses of ultrasound at this time produced permanent blocking of all C fibers. Again there was no change in the alpha and delta deflections.

Between the records in columns *B* and *C*, 11 additional series of irradiations, comprising 400 pulses at increasing intensities and durations, were administered. The delta fiber deflection (arrow), recorded with a faster sweep in column *C*, was somewhat diminished by this irradiation. At this point 20 0.7-second pulses at a plate voltage of 800 were administered. The delta response was permanently abolished by this more intense irradiation, but the alpha response remained unchanged (*5*).

Between the records in columns *C* and *D*, 160 more pulses of still longer duration were administered without apparent effect on the alpha deflection. The reduction in alpha response seen in column *D* was produced by 60 0.8-second pulses at a plate voltage of 800.

As illustrated by this experiment, there is an inverse relationship between fiber size and vulnerability to ultrasound in mammalian peripheral nerves. It was, however, seldom as clear-cut as in Fig. 1. Although small fibers were most sensitive to irradiation in all experiments, the degree of differential block varied considerably, and the ranges of dosage to which the different groups of fibers were sensitive often overlapped. Irradiation sufficiently intense to block C fibers usually affected conduction in some delta fibers as well. The alpha fibers were always most resistant. In general, the relationship between dosage and blocking was fairly linear throughout any one experiment, but the dosage levels required to produce equivalent effects in different experiments varied considerably. The inconsistencies were too large to be accounted for by biological variability. An explanation is being sought in further investigations of the physiological basis of ultrasonic blocking.

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1. R. R. Young and E. Henneman, *A.M.A. Arch. Neurol.* **4**, 83 (1961).
2. This investigation was supported by research grant No. B-970 from the National Institutes of Neurological Diseases and Blindness and by a research grant (DA-49-007-MD-523) from the Department of the Army to Dr. H. T. Ballantine, Jr., Massachusetts General Hospital.
3. The ultrasound (1.0 Mcy/sec) was generated piezoelectrically by excitation of a quartz crystal and focused with a polystyrene lens. It was transmitted through a saline-filled cone covered by a latex membrane into degassed mineral oil covering the nerve [See T. F. Hueter, H. T. Ballantine, Jr., W. C. Cotter, *J. Acoust. Soc. Am.* **28**, 192 (1956)].
4. The conduction speed of the fastest C fibers was found to be approximately 1 m/sec at 37°C.
5. The small deflection immediately following the alpha response in the lower records in Fig. 1 was caused by double firing of a few alpha fibers. It resulted from the intensity and duration of the stimulus required to excite the C fibers.

7 July 1961

Gonadotrophic Hormones Affect Aggressive Behavior in Starlings

Abstract. Injections of gonadotrophic hormones into subordinate male European starlings produced reversals in social rank, suggesting that pituitary gonadotrophic hormones rather than gonadal hormones influence aggressive behavior in this species.

The effects of gonadal hormones on the reproductive behavior of animals have been extensively studied (*1*). These hormones, androgens from the testes and estrogens from the ovaries, generally have proved to be very important in determining the characteristic behavior of each sex. Furthermore, the male hormone has long been recognized as a major determinant of aggressive behavior in animals (*2*).

In the European starling, *Sturnus vulgaris*, however, androgens apparently do not play a major role in determining aggressive behavior. Davis (*3*) found that castrated male starlings in the laboratory maintained song and fighting behavior for as long as a month after castration and, furthermore, that the social rank of individual starlings in the group was not affected by injections of testosterone. In addition, Hilton (*4*) and I (*5*) noted that there is a discrepancy between the yearly behavioral and gonadal cycles in male starlings. That is, both the weights of testes and the intensity of aggressive behavior reach a high point during the spring breeding season, and then decline during the summer. But aggressive behavior increases again in the fall even though gonadal weights remain at their minimal summer level. The apparent lack of relationship between androgen levels and aggressive behavior led to the investigation of behavioral effects of other hormones, and, as part of a more comprehensive study of pituitary activity in starlings, to an investigation of the effects of injected commercial gonadotrophins on aggressive behavior of caged male starlings, both intact and castrated (*6*).

In the first series of experiments, groups of five or six birds were placed together in a large flight cage and left together until a clear-cut social rank was evident (about 1 week). Then the lowest-ranking members of the group were given daily injections (for about 2 weeks) of Armour mammalian luteinizing hormone (LH). Administration of this hormone sometimes resulted in increased aggressiveness in the subordinate birds, but rarely in any increase in social rank. It was postulated that this failure to demonstrate behavioral changes might be attributed to learning; that is, once the social rank was established, the hormonal stimulus to change was not adequate to overcome the well-established, learned social rank. Consequently, the experimental procedure was redesigned in order to eliminate the effects of learning as much as possible.

In the new procedure, male birds, which had previously been kept in separate cages, were placed together in pairs in an observation cage just long enough to establish dominance of one over the other. The observation cage was a cubical box 3 feet square. It was lined with white oilcloth on three of its vertical sides; the fourth side was covered with hardware cloth so that, through a one-way mirror, the birds could be observed. The birds fought vigorously for the possession of the single perch. Control of this perch was the criterion of dominance. After dominance of one bird had been established (about 15 min), the subordinate bird was given LH and its behavior toward its cage partner was again observed (dominant birds were given saline injections). The first experiment was a pilot experiment to determine hormone dosages. Each pair consisted of a castrated male starling and an intact male bird, and, in five out of six pairs, the castrate was initially dominant. Reversals of dominance occurred in two cases upon injection of 250 μg and 900 μg of hormone, respectively. Bird 5, which was initially given 2000 μg of testosterone propionate, did not assume dominance after injection of either testosterone or luteinizing hormone. In the second experiment, castrated birds were initially dominant in 11 out of 12 pairs. When the subordinate birds were given 500 μg of LH, reversal of dominance occurred in six out of eight pairs. In the third experiment, every bird was successively paired with every other bird in the group. In this experiment, in contrast to the earlier experiments, the castrated birds were not always initially dominant. However, this experiment was done in March, when the pituitaries of intact birds show a high level of gonadotrophic activity (*5*). The results of these three experiments are summarized in Fig. 1.

In order to reduce the possible effects of learning even more, a fourth experiment was conducted with birds which were not paired to establish dominance before hormone injections were administered. In this case, only intact male birds were used. One of the birds in each pair was given 1000 μg of LH, the other saline; they were then placed together in the observation cage. If LH had no behavioral effects, one would expect the hormone-injected bird to dominate in 50 percent of the pairs and the saline-injected bird to dominate in 50 percent of the pairs. However, the hormone-injected birds were observed to dominate in 81 percent of the pairs; out of 16 pairs, there were two pairs in which no fighting occurred at all and one pair in which the saline-injected bird dominated. In 13 out of 16 pairs (81 percent) the hormone-injected bird dominated.

These experiments indicate that commercial luteinizing hormone from mammalian sources, when administered in large doses, can influence the aggressive behavior of caged male starlings. It is also of interest to note the rapid effect of the injections of this hormone on the behavior of the birds. Reversals of dominance, if they occurred at all, generally occurred within the first 10 to 15 minutes after injection. This rapid reaction indicates that perhaps the circulating hormone acts directly on behavioral centers in the brain. In addition, the dominance of castrated birds over their intact cage-mates is noteworthy. If LH is a determinant of aggressive behavior in the starling, as it appears to be, the aggressiveness of castrated birds may be a result of higher gonadotrophic activity in the pituitaries of castrates. Various workers, including Kato (*7*), working with chickens, found that castration increased the gonadotrophic activity of the pituitary.

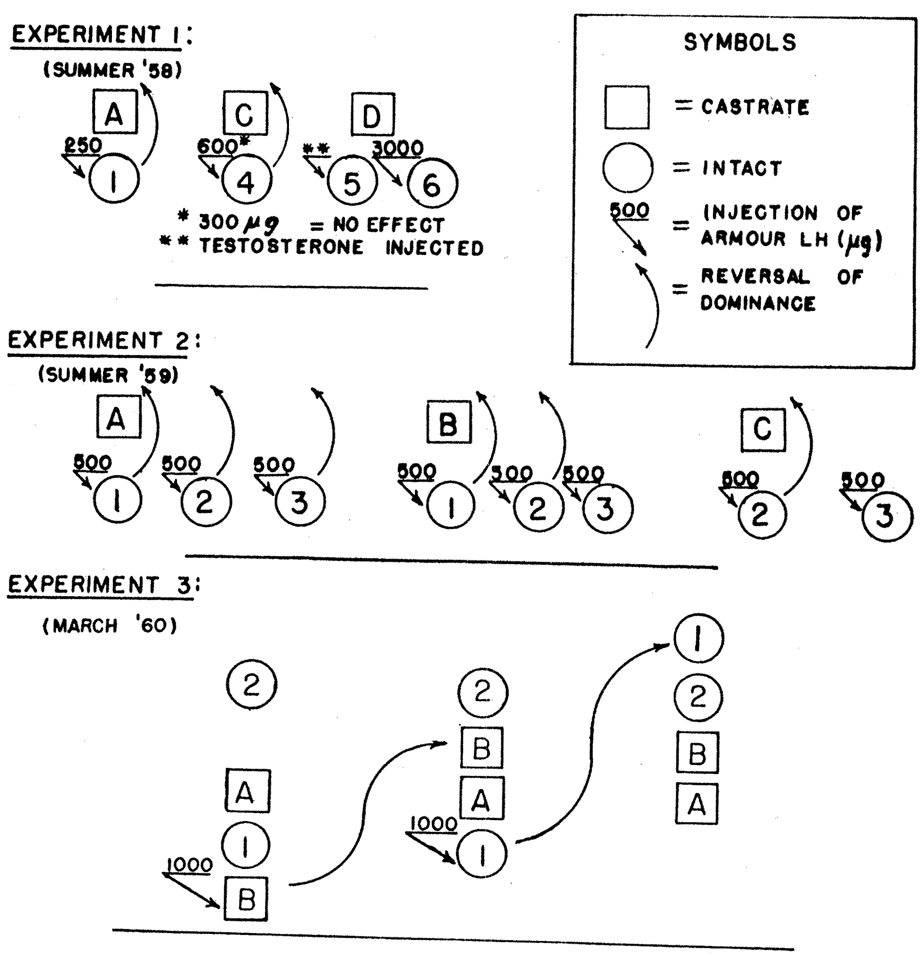

Fig. 1. Effects of hormone injections upon dominance of male starlings.

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26 May 1961