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Endocrine Control of Sexual Behavior in Mammals [1]

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The purpose of this report is to outline the present state of knowledge regarding the role of endocrines in controlling sexual behavior in mammals. It is apparent that any discussion of hormones and behavior must include not only direct but indirect actions of hormones, i.e. through their effects on metabolism, behavioral development, or modification of cognitive receptor pathways. An appreciation of the complexity of the regulatory factors underlying sexual expression can be obtained from the Figure which summarizes some of the interactions between endocrine, experiential, and perceptual factors. In the following review the major lines of evidence supporting the neuroendocrine basis of sexual behavior will be briefly summarized.

Endocrine control of neural organization underlying sexual behavior. It is logical to consider first the evidence which supports the possibility that the action of maternal or fetal hormones during gestation may have a role in determining sexual behavior at an early stage in development. It is known, for example, that some maternal hormones can cross the placental barrier. Injections of androgens and estrogens into pregnant rabbits, for example, have been shown to produce fetal intersexuality. The action of fetal hormones as important regulators of gonadal development is now fairly well established. In view of the fact that neural and reproductive differentiation occurs concomitantly, it would be reasonable to expect that fetal hormones also influence neural components of sexual behavior during embryonic development. Although this forms our rationale for believing that hormones affect neural organization, there is little evidence to substantiate this. The reason is that no quantifiable criterion of neural change is presently known through which neural-hormonal interactions can be assessed. Eayrs [3] has recently reviewed the literature available on hormones and neural maturation and has concluded that the fragmentary evidence 'does little more than suggest the lines of approach to future work'.

Most of the work on fetal hormones has been done on the following mammals by investigators from different laboratories: the opossum by Moore [4], the rat by Wells [5], the mouse by Raynaud [6], the rabbit by Jost [7], and the guinea pig by Dantchakoff [8]. All of these workers were primarily concerned with gonadal development rather than behavior.

Recently it has been shown that certain aspects of sexual behavior of adult guinea pigs can be modified through prenatal and postnatal administration of gonadal hormones [9]. For the most part, however, the degree to which adult sexual behavior depends upon hormones circulating in the fetus remains to be studied.

Role of sex hormones and experience as determinants of sex behavior. Let us now consider the problem of hormone-behavior relationship after reproductive maturity where much more information is available. The direct dependence of mating activity on the sex hormones has long been a subject of intensive study, and there is now no doubt that sex hormones play a cardinal role in the control of adult sexual behavior in most mammalian species. The exact mechanism of hormone action, however, remains obscure. Recently, emphasis seems to have turned from the role of hormones, to studies of the functional role of experience, in sexual behavior regulation. It was found that in some species, experience plays an equal, if not more important, role in the facilitation of sexual behavior than do the sex hormones.

Most of what is known regarding the action of hormonal or experiential 'determinants' of sex behavior has come from two broad areas of research: (1) studies of the normal physiology of reproduction in different mammalian species; (2) studies of the effects of the administration of pituitary gonadotrophins or gonadal hormones to immature and mature individuals.

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[4] C. R. Moore, *Embryonic Sex Hormones and Sexual Differentiation* (Thomas, Springfield, Ill. 1947).

[5] L. J. Wells, Arch. Anat. micr. Morph. exp. *39*, 499 (1950).

[6] A. Raynaud, *Modification expérimentale de la différentiation sexuelle des embryons de souris, par action des hormones androgènes et estrogènes* (Hermann et Cie, Paris 1942); Arch. Anat. micr. Morph. exp. *39*, 518 (1950); R. Soc. Biol. *127*, 993 (1938); Bull. Biol. France Belgique *72*, 297 (1938).

[7] A. Jost, Rec. Progr. Hormone Res. *8*, 379 (1953).

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[9] R. W. Goy, C. H. Phoenix, and W. C. Young, Anat. Rec. *131*, 559 (1938). – C. H. Phoenix, R. W. Goy, A. A. Gerall, and W. C. Young, Anat. Rec. *131*, 589 (1938).

The hypothesis currently advanced regarding the neuro-endocrine basis of sexual behavior is summarized in the succeeding paragraphs. Earlier experimental work which forms the basis for this hypothesis was summarized several years ago by BEACH[10].

First, to the best of our knowledge, *the basic neural components of sexual behavior are considered innate.* There is ample experimental documentation showing that sex-specific patterns of neural organization are already present at birth. Since male or female behavior can be elicited by the administration of the proper sex hormone shortly after birth, it must be assumed that the neural organization underlying sexual behavior is laid down independently of the action of sex hormones.

Second, among the factors known to influence the character of sexual behavior, *the gonadal hormones and experience play cardinal roles as determinants of mating activity in most, if not all, vertebrate species.* Relevant in this respect is the fact that the sex hormones do not exhibit absolute specificity. That is, although male and female hormones preferentially facilitate the normal mating behavior of their homotypic sex, each hormone can also facilitate the expression of sex behavior components of the opposite sex to a certain degree. It is important to emphasize that hormones are not responsible for the type of sex behavior of the organism; this presumably has an hereditary basis. The function of the sex hormones may be thought of as analogous to that of a 'film developer', i.e., merely acting to bring to expression an already predetermined innate behavioral repertoire.

Prior to 1942 there was a general tendency to relate differences in patterns of sexual activity to differences in levels of gonadal function. The present belief is that *sex hormones do not necessarily determine the level of sex drive,* although there is still some controversy on this. At any rate, in some species, such as the guinea pig, it appears that the level of the sex drive may largely be a function of the individual's genetic endowment. Exactly how sex hormones act to facilitate sexual expression, or how they establish the level of sex drive, remains a mystery. For the present we are forced to content ourselves with viewing these actions as threshold effects as suggested by GOLDSTEIN[11]. He postulated that gonadal hormones may have both a specific and a general effect on behavior, i.e., androgens may be thought as primarily acting to facilitate male behavior, and estrogens, female behavior, whereas both hormones also exert general non-specific facilitating effects on both sex patterns in the same animal.

From the limited number of mammalian species which have been studied, it would appear that certain components of sex behavior are common to most, or all, mammals. These include such activities as recognition and foreplay by both the male and female, lordosis, or 'presentation' by the female, and mounting, intromission, and ejaculation by the male. On the other hand, *considerable inter- and intra-specific variability may exist in the overall mating pattern.* So much so, even within closely inbred strains, that it is a common practice to use each animal as its own control in the study of endocrine-behavior interactions. That is to say, before one can measure the effect of a hormone on the sexual behavior of an animal, he must first establich the normal sex behavior level before treatment has been instituted. Some of the causes of variations in sex behavior of different species may be accounted for on the basis of: (1) differences in the degree to which the pre-determined sexual pattern is genetically established; (2) the relative importance of hormonal versus experimential factors regulating the completeness of frequency of normal mating activities; and (3) the temporal parameters of hormonal and experimential action. Although systematic studies of the time span over which sex hormones exert their actions have just begun, it may be forecast that this area of research will prove to be most fruitful.

There is no doubt that one of the most important contributions to our understanding of the role of endocrines in sex behavior was the demonstration that somatic factors determine or limit the nature of the physiological response to gonadal hormones[12]. Equally important was the relatively recent finding that experience in some species plays a much more important role than hormones in the final organization of sex behavior patterns[11,12].

In a recent report, YOUNG cited evidence that socially reared guinea pigs have a higher sex drive than littermates raised in isolation[12]. He further reported that the exact time at which the young are isolated from their companions may prove critical in some strains. Little difference was found in the sexual performance of isolated and socially raised males if isolation was instituted on day 25 postnatally. On the other hand, a marked reduction in sexual performance was obtained when males were weaned and isolated on day 10 instead of day 25. In earlier work, GRUNT and YOUNG[13] and also RISS *et al.*[14] found that although male hormone can restore sex behavior of castrate guinea pigs to preoperative levels, androgen injections were not found capable of augmenting sex behavior beyond the precastrate level. These workers reported that contact with other animals has an organizing

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[11] A. C. GOLDSTEIN, in *Hormones, Brain Function, and Behavior* (Acad. Press, N.Y. 1957), p. 99.

[12] W. C. YOUNG, in *Hormones, Brain Function, and Behavior* (Acad. Press, N.Y. 1957), p. 75.

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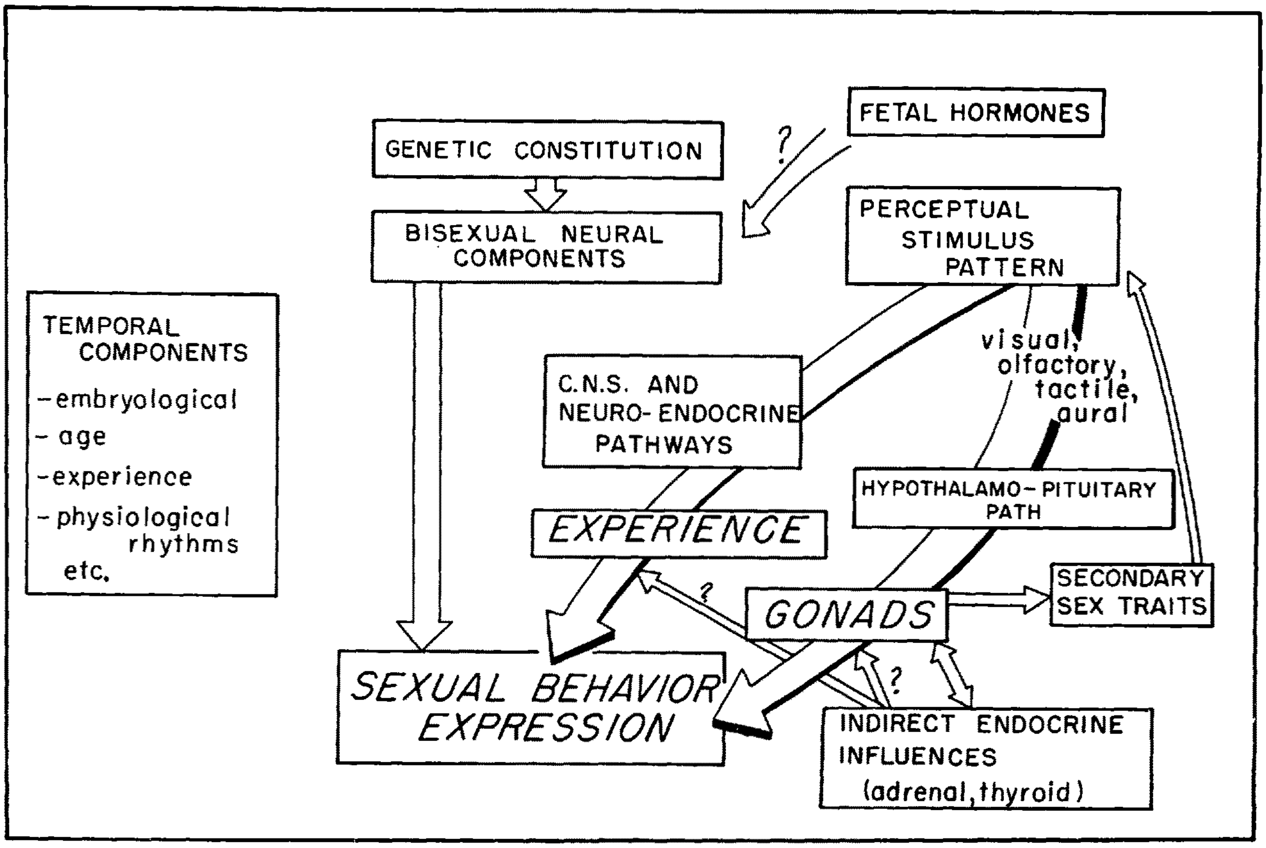

Regulatory mechanisms influencing sex behavior.

action on the development of the copulatory pattern in the male guinea pig. They also found that genetic differences in the level of sexual excitement are not overcome by large doses of androgen[14].

In the experiments using rats, however, BEACH and HOLZ-TUCKER[15] have reported that in the castrate rat, androgens not only restore mating behavior to the preoperative level but also cause an improvement in certain measures of sex behavior, if the maintenance dose of male hormone is exceeded. Recently, BEACH found no differences in the percentage of isolated and socially reared rats exhibiting completely organized sexual patterns on the first behavioral trial[16]. This indicates that, at least in the rat, experience is not essential for sexual behavior. On the other hand, ROSENBLATT and ARONSON report that in the male cat the mating pattern depends upon the combined influence of sexual experience and high androgen levels[17].

There are other differences in hormone-behavior regulatory mechanisms of the guinea pig and the rat. YOUNG[18] found that the mounting occurs only at estrus in female guinea pigs and is abolished by ovariectomy. BEACH[19] reports that in female rats, mounting occurs throughout the entire estrous cycle and persists after ovariectomy. Paradoxical findings such as these point to the need for more experimental work on behavioral effects of hormones in different mammalian species.

Appropriate in this regard are a number of studies dealing with the effects of experience and hormones in the domestic fowl[20]. Most of the reported findings support the belief that the degree of social experience affects the level of sexual expression in birds. On the basis of their current work with turkeys, however, SCHEIN and HALE state that transient test conditions rather than differential social and sexual experience may contribute to the apparent differences in levels of response[21]. From their work on turkeys they believe that levels of sexual expression are not dependent upon the degree of early social experience. One must conclude that the problem of the relative importance of experience and hormones in controlling sexual behavior is still not completely resolved for either mammals or birds.

Apart from the known dependence of the neurohumoraly regulated ovulatory response on coitus in the

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[16] F. A. BEACH, J. comp. Physiol. Psychol. *51*, 37 (1958).

[17] J. S. ROSENBLATT and L. R. ARONSON, Anim. Behav. *6*, 171 (1958).

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[20] D. G. M. WOOD-GUSH, Anim. Behav. *6*, 68 (1958); Proc. R. physiol. Soc. Edinburg *27*, 6 (1958).

[21] M. W. SCHEIN and E. B. HALE, Anat. Rec. *128*, 617 (1957); Poult. Sci. *37*, 1240 (1958); unpublished data.

cat, rabbit, and ferret, there is no information presently available which directly relates to the influence of animal interactions during mating on the endocrines. There is no doubt that during the sexual encounter there occur marked shifts in the secretory activity of such glands as the adrenal and thyroid. To what extent sexual behavior is in turn modified by the nature of the endocrine response still remains to be investigated.

Indirect endocrine influence on sex behavior. BEACH[22] has pointed out that all hormones which affect metabolic processes of tissues will exert some indirect effect on sex behavior.

Because of the close interactions between the adrenals and gonads[23], and the thyroids and gonads[24], adrenocortical and thyroid secretions have long been suspected of influencing the responsiveness of tissues mediating sex behavior. There is considerable evidence that *abnormal* thyroid or adrenal function may have profound effects on sexual behavior. Thus far, however, there is little direct evidence bearing on the problem of whether sexual behavior is closely correlated with adrenal or thyroid function under normal conditions. Several attempts to define the nature of thyroid effects on sexual performance have not met with much success. YOUNG[25] reports that sexual behavior in the guinea pig is relatively unaffected by injections of thyroid hormone, or by thyroidectomy; HEIDENREICH[26] obtained similar results using rats. WARREN and ARONSON[27] found that prepuberal castration of male hamsters does not prevent the development of some aspects of the sexual pattern. These workers also found that the behavior of the hamster that is both castrated and adrenalectomized before maturity is essentially the same as that of the simple castrate. It should be pointed out, however, that except for a few such studies there are no quantitative data available on behavioral changes as a function of changes in thyroid or adrenal activity.

One generalization which can be drawn is that sexual performance is dependent upon the adequate functioning of many organs and tissues. The most important endocrine organ to which has been delegated the duty of maintaining tissue homeostasis is the adrenal cortex. Since adrenal activity may be influenced by a variety of conditions including nutritional state, temperature fluctuations, age, and even daily activity rhythms, it would be reasonable to expect some relationship between adrenal activity and sexual performance. Unfortunately, there is insufficient evidence to even speculate as to the degree that sexual responsiveness may depend on such indirect endocrine influences.

There would appear to be important advantages of working on the hormone-behavior problem in seasonal breeders. An experimental analysis of the seasonally breeding prairie dog by ANTHONY[28] showed that there was a close correspondence between increased activity of animals, changes in adrenal function, and the onset of breeding, indicating that adrenal influence may have an important role in regulating mating behavior. ANTHONY[29] also observed that cage confinement inhibits mating behavior, despite the fact that there is no observable effect on gonadal development, which supports the belief that the sex hormones are not the sole regulators of sexual behavior in some species.

Résumé

L'auteur présente une revue critique des bases expérimentales de l'hypothèse neuro-endocrine du comportement sexuel des mammifères.

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Brèves communications - Kurze Mitteilungen
Brevi comunicazioni - Brief Reports

High Pressure Preparation and Structure of Crystalline Nickelous Carbonate**

LANGLÈS[1] recently succeeded in preparing crystalline $NiCO_3$ for the first time. He obtained two forms, depending on the reagents used and the conditions of precipitation. The two forms possessed somewhat different lattice constants, but belonged to the same space group. Consequently, a polymorphic transition is unlikely. It is possible that his material might have been of slightly inferior purity.

In the present study colloidal $NiCO_3$ was precipitated from aqueous solutions of nickelous sulfate and sodium

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