

Section A

Ans.Options for MCQ

i- c; ii- c; iii-c; iv-b; v- b; vi- b; vii- a; viii- b; ix- b ; x- b

Section B

Answer 1 . Gonadotropes are those endocrine cells of the anterior pituitary gland that produce **gonadotropins**

Gonadotropes appear basophilic in histological preparations. There are two types of **gonadotropin**

1. Follicle stimulating hormone (FSH) and
2. Luteinizing hormone (LH).

Release of FSH and LH is regulated by gonadotropin releasing hormone represented as GnRH secreted from the hypothalamus.

Structure FSH and LH: FSH- glycoprotein. Its structure is similar to that of LH, The protein dimer contains 2 polypeptide units, labeled alpha and beta subunits. The alpha subunits of LH, FSH, TSH, and hCG are identical, and contain 92 amino acids. The beta subunits vary. FSH has a beta subunit of 111 amino acids (FSH β), which confers its specific biologic action and is responsible for interaction with the FSH-receptor. The sugar part of the hormone is composed of fucose, galactose, mannose, galactosamine, glucosamine, and sialic acid, the latter being critical for its biologic half-life. The half-life of FSH is 3–4 hours.

Gene of FSH alpha subunit gene is located on chromosome 6p21.1-23 and beta subunit is located on chromosome 11p13, and is expressed in gonadotropes of the pituitary cells, controlled by GnRH, inhibited by inhibin, and enhanced by activin

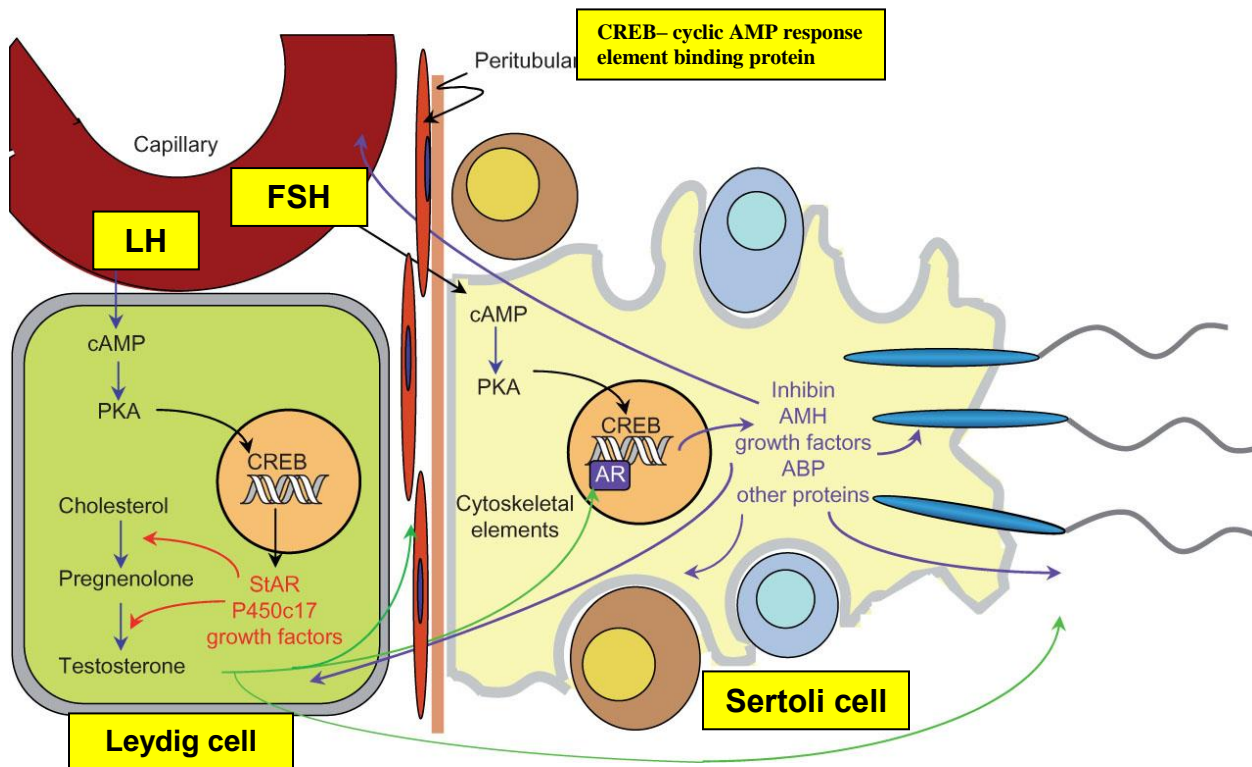
LH -is a heterodimeric glycoprotein. Each monomeric unit is a glycoprotein molecule; one alpha and one beta subunit. The protein dimer contains 2 glycopeptidic subunits, labeled alpha and beta subunits, that are non-covalently associated (i.e., without any disulfide bridge linking them):

- The alpha *subunits* of LH, FSH, contain 92 amino acid residues in human In other vertebrate species 96 amino acids however in invertebrates glycoprotein hormones do not exist.
- The *beta subunits* vary. LH has a beta subunit of 120 amino acids (LHB) that confers its specific biologic action and is responsible for the specificity of the interaction with the LH receptor.

The beta subunit contains an amino acid sequence which exhibits maximum homologies with the beta subunit of human Chorionic Gonadotropin. However, the hCG beta subunit contains an additional 24

amino acids, and the two hormones differ in the composition of their sugar moieties. The biological half-life of LH is 20 minutes, shorter than that of FSH (3–4 hours) and hCG (24 hours). LH Gene for the *alpha subunit* is located on chromosome 6q12.21 and *beta subunit* gene is localized in the LHB/CGB gene cluster on chromosome 19q13.32. Beta LH subunit gene activity is restricted to the pituitary gonadotropic cells. It is regulated by the gonadotropin-releasing hormone from the hypothalamus. Inhibin, activin, and sex hormones do not affect genetic activity for the beta subunit production of LH.

Secretion and Regulations



2. Answer2: Spermatogenesis: Two important cell types in seminiferous tubules

- A. Germ cells– In various stages of sperm development, such as spermatogonia, primary spermatocytes, secondary spermatocytes
- B. Sustentacular (Sertoli) cells– these cells provide crucial support for spermatogenesis

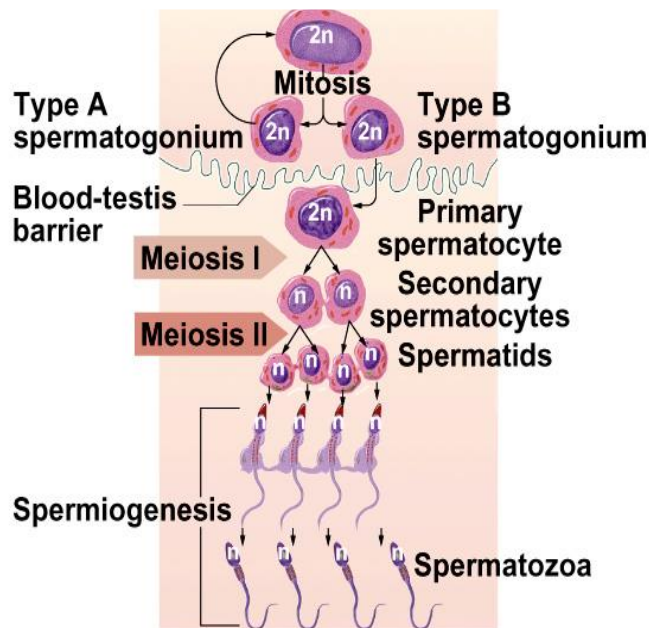
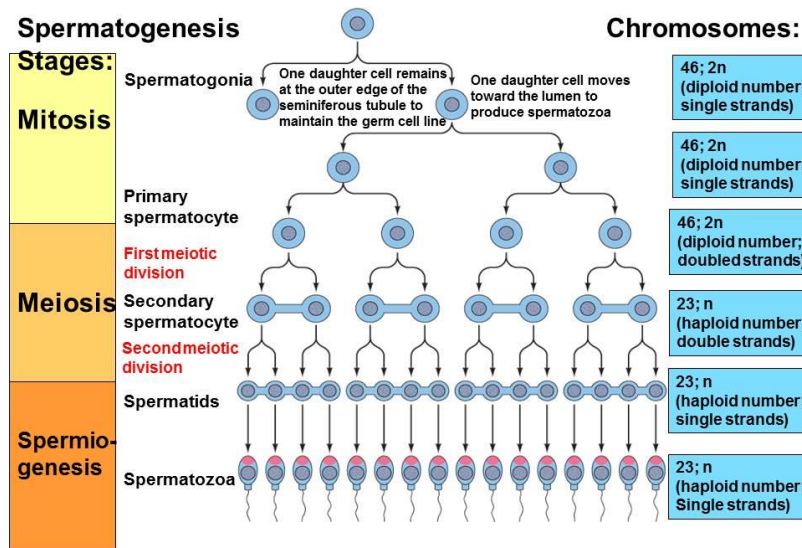
3. Three major stages—

- A. Mitotic proliferation—
- B. Spermatogonia located in the outermost layer of the seminiferous tubule, outside the blood-testis barrier (BTB)

- C. One of the daughter cells (Type A spermatogonium) remain at the outer edge of the tubule. The other daughter cell (Type B spermatogonium) starts moving toward lumen forming 4 identical primary spermatocytes (2N)

Meiosis—Each primary spermatocyte (2N) must pass through BTB (tight junction) and ultimately yield 4 spermatids (1N) **Spermiogenesis**—

- Spermatids become extremely specialized and motile spermatozoa
- Sperm travel lightly



Endocrine Regulation

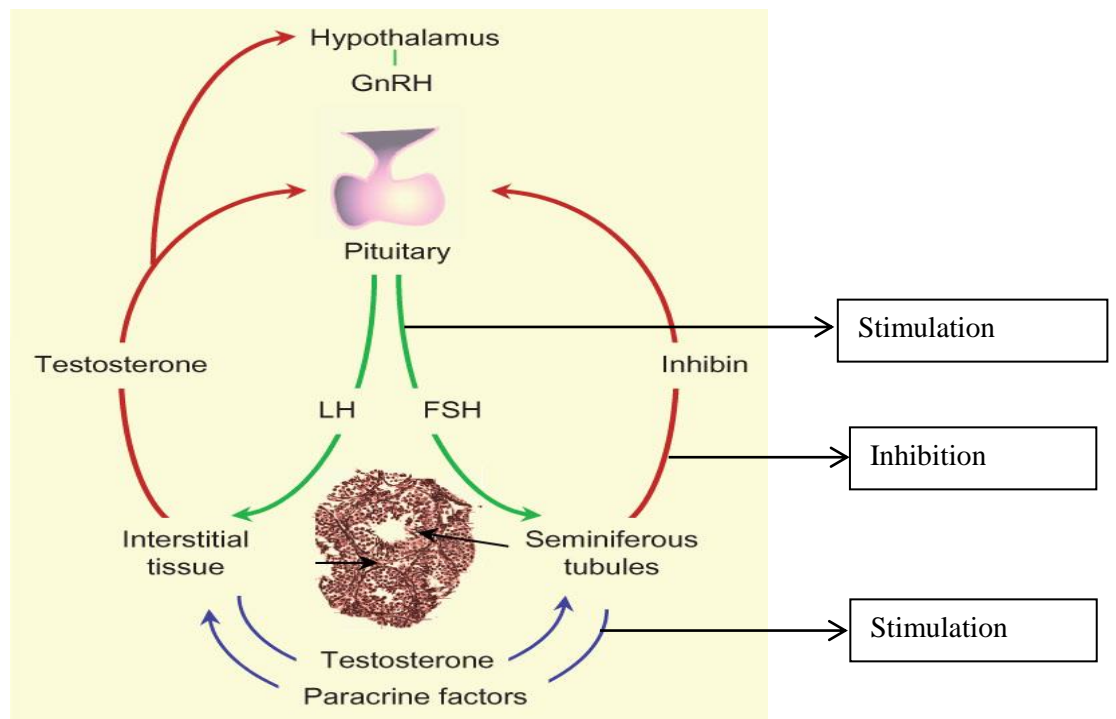
1. Sertoli cells– only cells known to express FSH receptors in human males; also have testosterone receptors
2. FSH, LH, and testosterone all play vital roles in spermatogenesis.

Mechanism of action by Testosterone

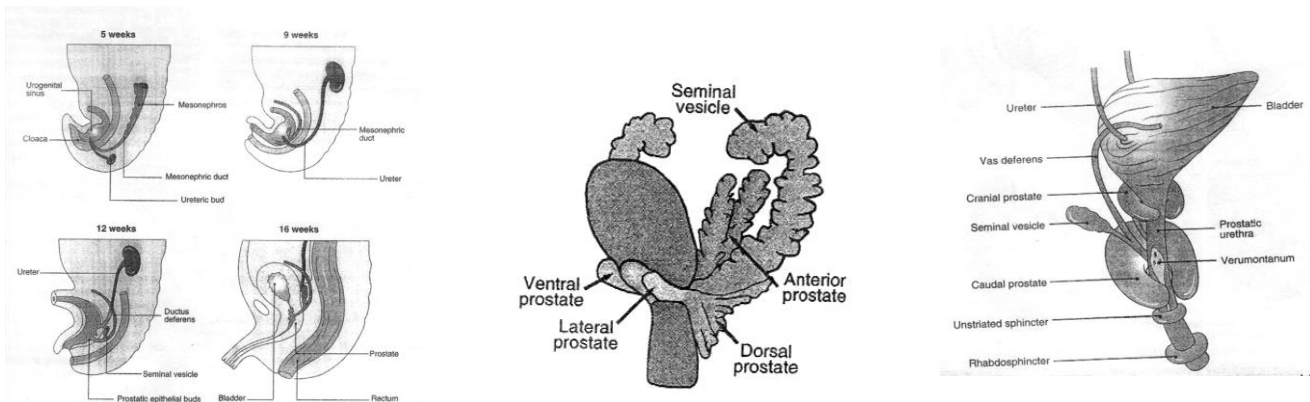
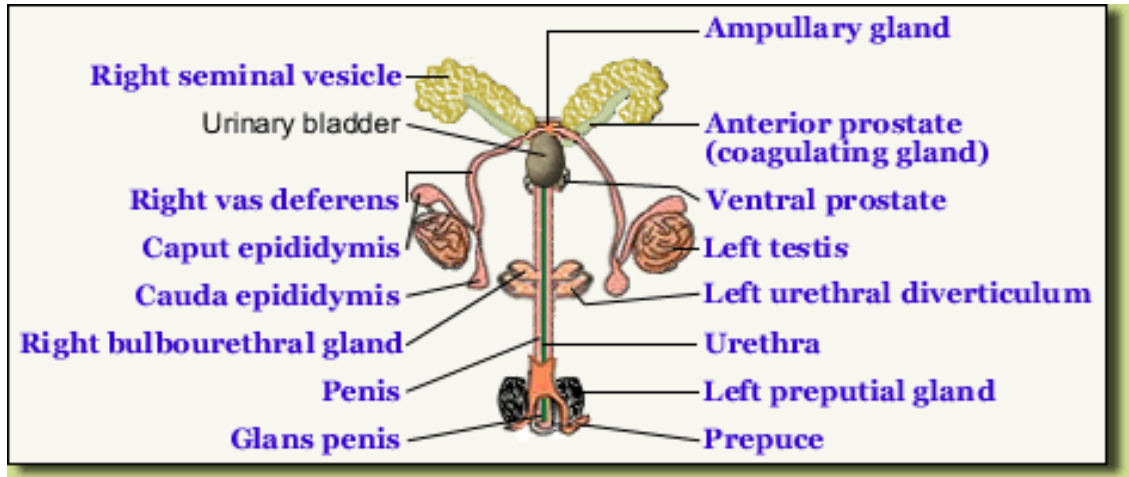
- a. Nuclear receptors-- Testosterone (T)** often converts to 5 α -dihydrotestosterone before binding to their nuclear receptors
- b. T also may bind to membrane receptors--** either directly or through the bind of the sex hormone binding globulin

NEGATIVE FEED BACK REGULATORS - HYPOTHALAMUS - PITUITARY - TESTES

1. Hypothalamus GnRH– stimulates secretion of both LH and FSH
2. Testosterone, which is secreted in response to LH, acts as a feedback regulator of LH.
3. FSH stimulates the Sertoli cells to synthesize and secrete inhibin (glycoprotein), which regulates FSH secretion



Question 4: Development and structural organization of Prostate gland

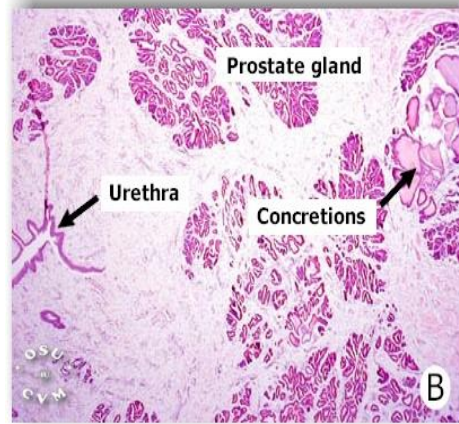
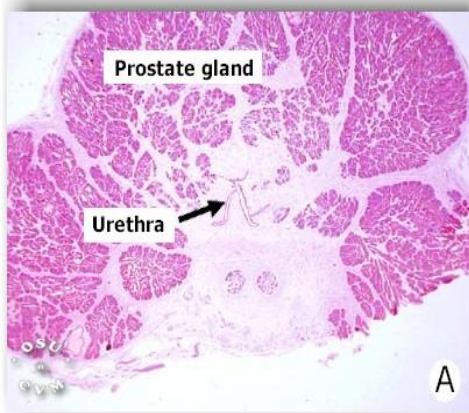


The prostate -contains separate lobes: dorsal, lateral (the dorsal and lateral lobes are frequently combined as dorsolateral), ventral, and anterior (coagulating gland). All lobes consist of branching blind-ending tubules that are surrounded by a thin fibromuscular layer; between the tubules (glands) is loose connective tissue. The prostate glands contain luminal secretory, basal, and neuroendocrine (<0.3%) cells, but the basal and neuroendocrine cells can be identified by light microscope only after immunostaining for a cell-specific marker (e.g., keratin 5 for basal cells, chromogranin for neuroendocrine cells). The secretions of the prostate glands are carried by ducts to the colliculus seminalis.

A characteristic feature of the prostate is the appearance of *corpora amylacea* in the secretory alveoli. They are rounded eosinophilic bodies. Their average diameter is about 0.25 mm (up to 2 mm). They appear already in the seventh month of foetal development. Their number increases with age - in particular past 50. They may undergo calcification. Corpora amylacea may appear in

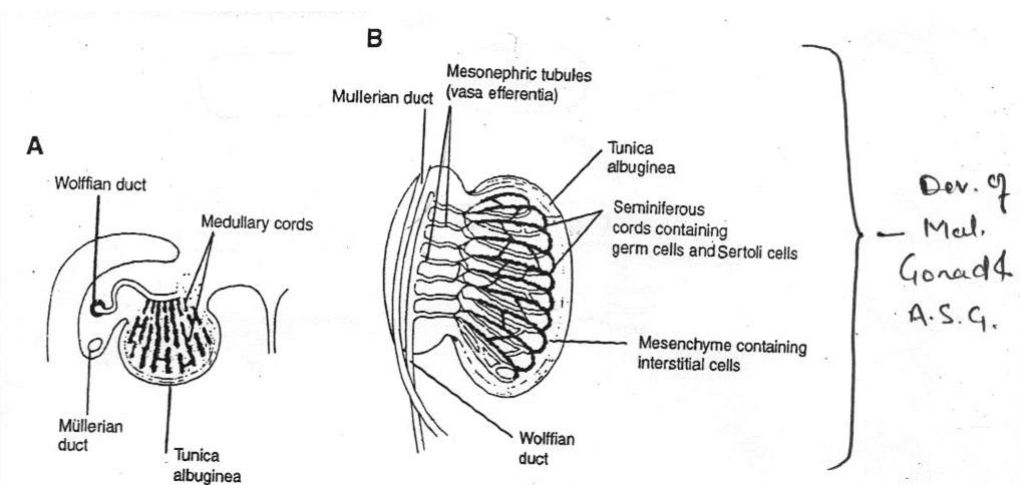
semen. Microscopically the prostate can be divided into lobes, but they are inconspicuous in histological sections. In good histological sections it is possible to distinguish three concentric zones, which surround the prostatic part of the urethra.

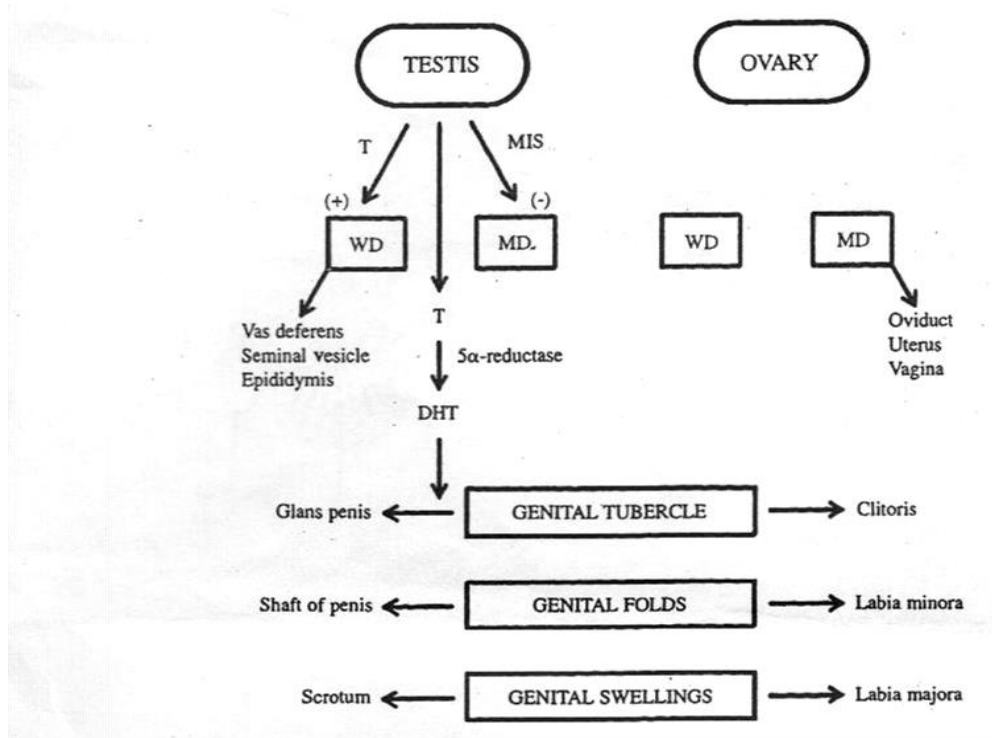
- The peripheral zone contains large, so-called *main glands*, whose ducts run posteriorly to open into the urethra.
- The internal zone consists of the so-called *submucosal glands*, whereas
- the innermost zone contains *mucosal glands*.



Histological section (HE) of prostate gland

Question 5: hormonal regulation of gonadal and brain development in mammals





Sexual differentiation is the process of development of the differences between males and females from an undifferentiated zygote (fertilized egg).

Sex differences may be induced by specific genes, by hormones, by anatomy, or by social learning. Some of the differences are entirely physical (e.g., presence of a uterus) and some differences are just as obviously purely a matter of social learning and custom (e.g., relative hair length). Many differences, though, such as gender identity, appear to be influenced by both biological and social factors ("nature" and "nurture").

The early stages of human differentiation appear to be quite similar to the same biological processes in other mammals and the interaction of genes, hormones and body structures is fairly well understood. In the first weeks of life, a fetus has no anatomic or hormonal sex, and only a karyotype distinguishes male from female. Specific genes induce gonadal differences, which produce hormonal differences, which cause anatomic differences, leading to psychological and behavioral differences, some of which are innate and some induced by the social environment.

Y chromosome must carries a gene which determines testicular formation (originally termed *TDF*) referred as *SRY*, has been found to direct production of a protein which binds to DNA, inducing differentiation of cells derived from the genital ridges into testes. In transgenic XX mice (and some human XX males), *SRY* alone is sufficient to induce male differentiation. Further literature suggests that human sex reversal (XX males, XY females) has led to discovery of other genes crucial to testicular differentiation on autosomes e.g., *WT-1*, *SOX9*, *SF-1*, and the short arm of X (*DSS*).

The Effects of Prenatal Hormones on Sexual Development : XX & XY – first 6 weeks of life all embryos are female

1. Primordial gonads

- a. Mullerian system – Female, destined to form female internal organs & female external genitalia
- b. Wolffian system – Male equivalent, destined to form male internal organs & male external genitalia

Human prenatal sexual differentiation

Fetal age (weeks)	Crown-rump length (mm)	Sex differentiating events
0	blastocyst	Inactivation of one X chromosome
4	2-3	Development of wolffian ducts
5	7	Migration of primordial germ cells in the undifferentiated gonad
6	10-15	Development of müllerian ducts
7	13-20	Differentiation of seminiferous tubules
8	30	Regression of müllerian ducts in male fetus
8	32-35	Appearance of Leydig cells. First synthesis of testosterone
9	43	Total regression of müllerian ducts. Loss of sensitivity of müllerian ducts in the female fetus
9	43	First meiotic prophase in oogonia
10	43-45	Beginning of masculinization of external genitalia
10	50	Beginning of regression of wolffian ducts in the female fetus
12	70	Fetal testis is in the internal inguinal ring
12-14	70-90	Male penile urethra is completed
14	90	Appearance of first spermatogonia
16	100	Appearance of first ovarian follicles
17	120	Numerous Leydig cells. Peak of testosterone secretion
20	150	Regression of Leydig cells. Diminished testosterone secretion
24	200	First multilayered ovarian follicles. Canalisation of the vagina
28	230	Cessation of oogonia multiplication
28	230	Descent of testis

In a male fetus, testes produce steroid and protein hormones essential for internal and external anatomic differentiation. **Leydig cells begin to make testosterone by the end of month 2 of gestation.** From then on, male fetuses have higher levels of androgens in their systemic blood than females. The difference is even greater in pelvic and genital tissues. Antimüllerian hormone (AMH) is a protein hormone produced

by Sertoli cells from the 8th week on. AMH suppresses development of müllerian ducts in males, preventing development of a uterus

Brain Differentiation

Differences of exposure of a fetal or infant brain to sex hormones produce significant differences of brain structure and function which correlate with adult reproductive behavior. This seems to be the case in humans as well; sex hormone levels in male and female fetuses and infants differ, and both androgen receptors and estrogen receptors have been identified in brains. Several sex-specific genes not dependent on sex steroids are expressed differently in male and female human brains. Structural sex differences begin to be recognizable by 2 years of age, and in adult men and women include size and shape of corpus callosum and certain hypothalamic nuclei, and the gonadotropin feedback response to estradiol

Question 6: Gonadal hormones, their functions and site of action

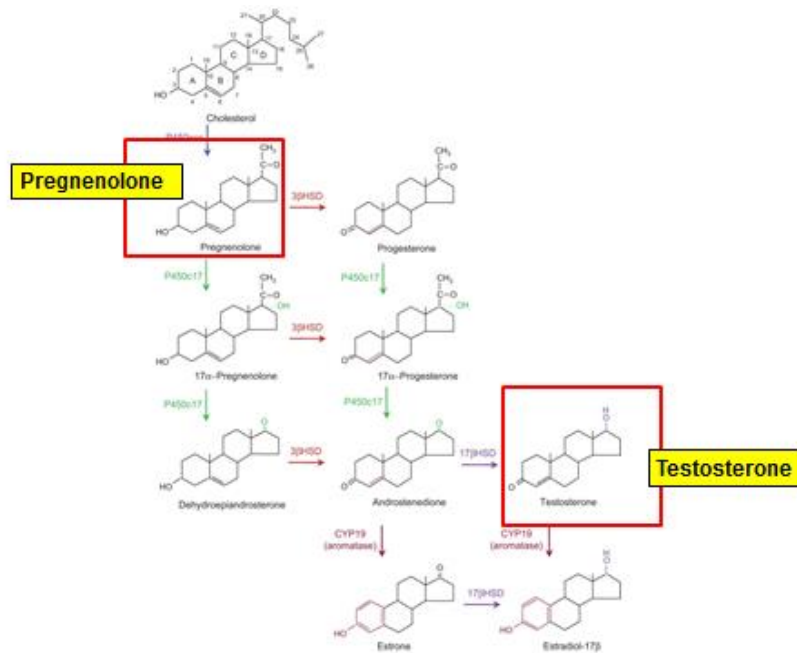
Gonadal hormone

- The main steroid produced in the male is testosterone, from the testis. In addition, the testis makes some androstenedione, dihydrotestosterone, and estradiol.
- In the male, there is peripheral conversion of testosterone to dihydrotestosterone -in androgen target tissues, like muscle and estradiol mostly in adipose tissue).
- - seminiferous tubules: production of sperm cells, location of Sertoli cells (stay tuned...)
- - interstitial tissue: outside of the seminiferous tubules; the steroidogenic cell is the Leydig cell. Leydig cells: respond to luteinizing hormone (LH) with steroid production (primarily testosterone).
- enzymes/pathways for producing androgens and estrogens are utilized in adrenal, testis, and ovary, you will be expected to know the names of these enzymes, and their role (example; know that 3b-HSD converts pregnenolone into progesterone).
- The ovary produces estrogens (primarily estradiol), progesterone, and androgens. Ovarian steroids are secreted primarily from ovarian follicles and corpora lutea.

Product	Functions
Progesterone	prepares uterus lining for implantation of ovum
Androgens (strongest = testosterone)(produced in testes primarily but weak androgens in adrenal cortex) (anabolic steroid)	development of male secondary sex characteristics; prevents bone resorption
Estrogen (produced in ovaries primarily but also in adipose cells of males and females)	development of female secondary sex characteristics; prevents bone resorption

Steroidogenic Enzymes

Common name	"Old" name	Current name
Side-chain cleavage enzyme; desmolase	P450 _{SCC}	CYP11A1
3 beta-hydroxysteroid dehydrogenase	3 beta-HSD	3 beta-HSD
17 alpha-hydroxylase/17,20 lyase	P450 _{C17}	CYP17
21-hydroxylase	P450 _{C21}	CYP21A2
11 beta-hydroxylase	P450 _{C11}	CYP11B1
Aldosterone synthase	P450 _{C11AS}	CYP11B2
Aromatase	P450 _{aro}	CYP19

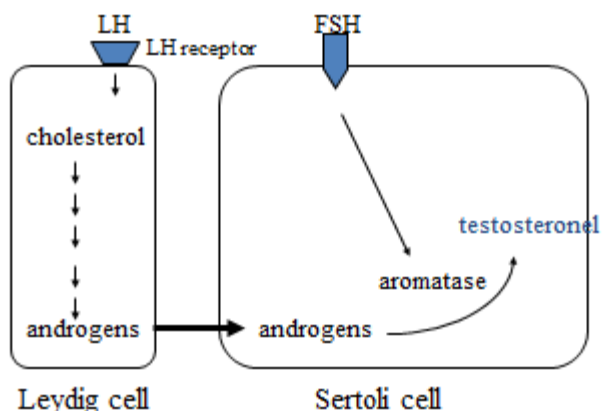


Steps of testosterone synthesis-

Four other enzymes convert pregnenolone (21 C) to testosterone (19 C)

The Two-Cell Theory

- Numerous studies have now shown that the androgens required for aromatization come from the neighboring theca cells:



Question 7: Role of hormone and neurons of Central Nervous system during brain and behavioural differentiation in vertebrate male and female

- Hormones modify behavior by affecting**

- Sensory or perceptual mechanisms
- Development or activity of the central nervous system, and
- Muscles important in the execution of behavior

- Hormones influence the ability to detect certain stimuli**

- And the responses to and preferences for particular stimuli

- In some species, mate choice is based on hormone-mediated differences in the ability to detect stimuli**

- Female domestic pigs are attracted to the boar(雄猪) pheromone, 16-androsterone, while males are not
- Castrated males given the female hormone estradiol show female responses to a boar

- Hormones can mediate behavioral responses to stimuli**

- Vasotocin: a peptide hormone in non-mammalian vertebrates similar to the mammalian hormone vasopressin Vasotocin enhances male responsiveness to female stimuli**

- Male newts first rely on visual cues (i.e. size, shape, and color)
- Then switch to olfactory cues for close-up confirmation of species, gender, and reproductive state

3. The male clasps the gravid female for hours in amplexus

- The female becomes sexually receptive

Hormones can cause a change in preference in animals

1. Sex steroids can change social preferences
2. Given a choice of social partner, young animals that received parental care prefer family members
3. As they mature, they prefer non-family members

■ **Hormone-mediated changes in social preference are not limited to maturing animals**

1. In winter, adult female meadow voles prefer other females
2. During mating season (spring and summer), they prefer males
3. This reversal in preference is caused by higher estrogen levels, associated with longer days

Effects on development and activity of the central nervous system

- Circulating hormones affect behavior by influencing the central nervous system
- They influence different regions of the brain, including the
 - (1) volume of brain tissue
 - (2) number of cells in brain tissue
 - (3) size of cell bodies
 - (4) extent of dendritic branching
 - (5) percentage of neurons sensitive to particular hormones
 - (6) survival of neurons
- **Transfer of internal information by the endocrine system occurs slowly, with general, long-lasting effects**
- Communication occurs through hormones and neurohormones that produce changes at the cellular level .That ultimately influence behavior. Two types of hormones are peptide and steroid hormones
 - Hormones influence behavior by affecting: sensation, the central nervous system, or muscles responsible for the execution of behavior
 - Effects of steroid hormones on behavior have been divided into organizational and activational effects Hormonal effects on behavior can be studied by interventional studies or correlational studies
 - Hormones initiate changes in behavior and behavior can causes changes in levels of hormones
 - Interactions between hormones and behavior are sensitive to the physical and social environment
 - Behaviors mediated by hormones include
 - Aggression, courtship, mating, caring for young, scent-marking, and migrating

Hormones influence development of singing behavior in birds

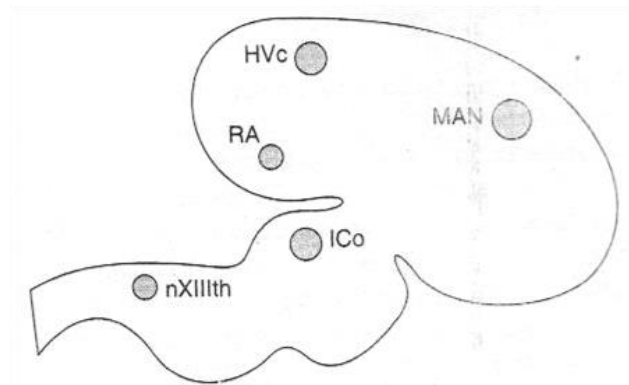
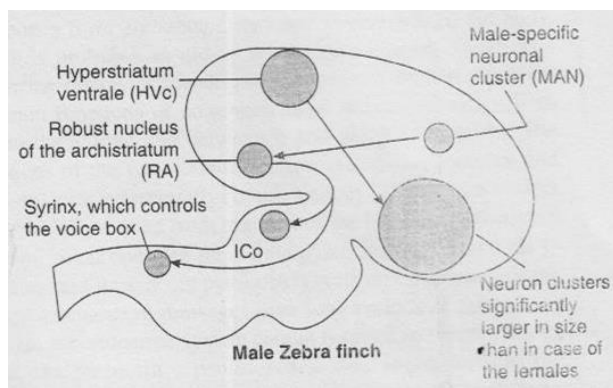
-In the zebra finch, sex differences in the brain nuclei that control song are established around the time of hatching Soon after hatching, the brain's hormonal environment establishes sex differences in adult singing behavior (males sing and females do not)

M Sc Third Semester Zoology Examination 2013; Spl paper II
Mammalian Reproductive Physiology & Endocrinology **Male Reproduction**

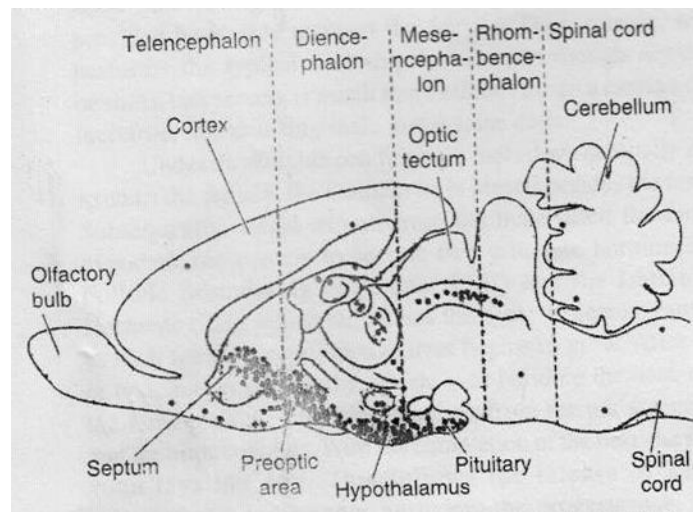
-The steroid hormones involved in the early masculinization of the zebra finch brain are neurosteroids, not gonadal steroids

Hormones affect muscles and motor neurons

- South African clawed male frogs emit six different calls
- The advertisement call allows females to find males
- Sexually receptive females produce a rapping call
- Unreceptive females tick
- Hormone-induced changes in the muscles of the larynx results in sex differences in calling behavior



Female Zebra finch



Representation of estrogen binding receptor in female brain

Testosterone and estrogen sensitive neuron are reported which are located in the neural circuits and known to mediate reproductive behavior via hypothalamus and pituitary.

Question 8: Different copulatory pattern among vertebrates

Copulatory Behavior: The union of male and female gametes can take place externally, as it does in many amphibians and fish that release their eggs and sperm into the water, or it can occur internally as it does in mammals, birds, and many fish and insects. Both forms require precisely timed movement patterns to assure that fertilization occurs. This lesson will focus on the copulatory behavior of mammals. We will begin by describing the various movement patterns involved in copulation and how these patterns vary among species. Then we will review ideas concerning the reasons for the enormous variability that exists.

Patterns of Copulation: Male Behavior

The diversity of mammalian copulatory behavior is illustrated by a classification scheme for the copulatory behavior of male mammals developed by Donald Dewsbury of the University of Florida.

The classification is based on four features that are either present or absent in copulatory behavior, resulting in **sixteen categories of behavior divided in four different stages**. They are:

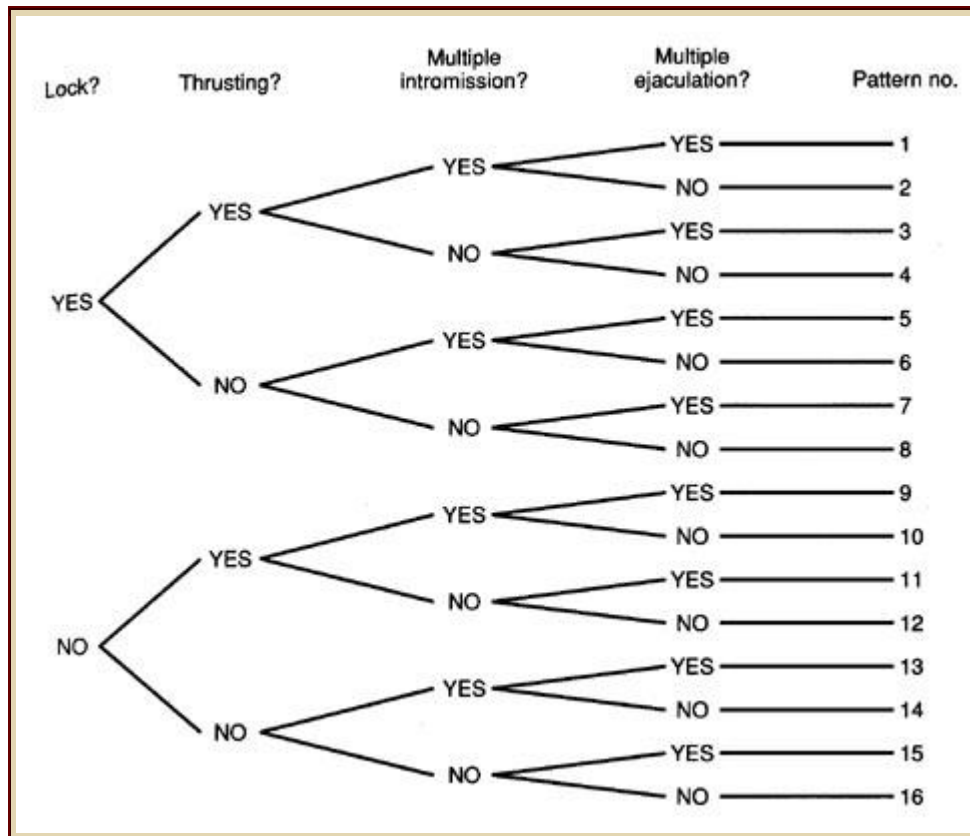
- (1) Lock: Some species, such as domestic dogs, exhibit a vaginal lock following ejaculation. The penis swells, making withdrawal difficult or impossible.
- (2) Thrusting: In some species, such as humans, the penis is repetitively thrust back and forth in the vagina. In others, there is no intra-vaginal thrusting.
- (3) Intromission frequency: In some mammals, such as rats, the male mounts the female, intromits the penis into the vagina, and then quickly dismounts. Rats must intromit several times before an ejaculation can occur. Other species need intromit only once.
- (4) Ejaculation frequency: In some species, such as baboons, the male typically ejaculates several times per copulation episode. Others usually ejaculate only once.

Each species is classified according to its performance on each of the four variables. Although eleven of the sixteen possible categories have been discovered in at least one species, even closely related species may fit into different slots in this system. For example, seven of the sixteen categories were found in a survey of thirty-one species of small rodents. Primates are less diverse than rodents in their copulatory patterns, with only three of the sixteen patterns known so far. Why these species differences exist is not yet known. No ecological correlation of any note has been discovered, and the finding that there is no evolutionary pattern makes the whole thing even more puzzling. Obviously, more data are necessary to enlighten this issue.

Female Behavior

The classification of female mammal copulatory behavior is not as far advanced. Studies of female copulation have emphasized the behaviors used by females to initiate copulation and the female's postures and movements during mounting and intromission. There are species-typical patterns in all these behaviors, but the classification has been applied only to rodent species. Not surprisingly, female behavior patterns complement those of males, so there are species differences in female patterns that parallel those of males. Much more information is needed on female behavior and on the coordination of the interaction of male and female during copulation.

Orgasm is a component of female copulatory behavior that has often been thought to occur only in humans. Recent evidence, however, establishes the existence of female orgasm, at least in non-human primates, although the physiological details vary among species.



Quantitative Differences in Copulatory Behavior

Species that fall in the same pattern category often differ quantitatively in their behavior. For example, the number of intromissions per ejaculation may vary, the average amount of time that elapses between intromissions or ejaculations may differ, and so on. For example, although hamsters and rats display pattern 9 (no lock, thrusting, multiple intromissions, and multiple ejaculations), in hamsters the average amount of time between mounts with intromission is about ten seconds or less, but in rats this interval is about fifty to 100 seconds. Furthermore, the duration of both intromission-only mounts and ejaculatory mounts is much longer in hamsters than in rats.

The existence of many different copulatory patterns and so much variation in the quantitative aspects of copulation cry out for an explanation. However, copulation looks more like some complex dance, carefully timed and choreographed. Why?

One explanation has emphasized some basic processes of female reproductive physiology, especially ovulation and implantation. Most mammalian species release eggs (ovulate) spontaneously; that is, hormonal changes in the female lead to ovulation even if copulation has not occurred. Humans and rats are spontaneous ovulators. Other species are induced ovulators, releasing eggs only if copulation has taken place. This is due to the tactile stimulation associated with copulation, specifically that applied to the vagina by the penis. Thus, ovulation occurs only when there is a high likelihood of fertilization occurring. Rabbits, cats, and some rodents are induced ovulators.

Another way that copulation facilitates pregnancy is to prepare the uterus for implantation of the fertilized ova. For example, in the absence of the usual copulatory pattern, female rats will slough off fertilized ova.

This is because the tactile stimulation provided by intromission triggers hormonal changes required for implantation.

Other hypotheses for the existence of complex copulation suggest that the precise details of copulation are linked to other aspects of the physiology of the female reproductive system. For example, sperm motility in the female reproductive tract of rats is slowed if intromissions are not adequately spaced in time. As another example, hamsters (which have multiple intromissions and multiple ejaculations) require at least four "ejaculatory series" (a series includes the intromission with ejaculation plus all the intromission-only mounts that preceded it) in order for pregnancy to result with high probability. Additional series do not increase the probability of pregnancy occurring, nor do they increase the number of pups in the litter.

Quantitative differences in copulation may foster reproductive success in other ways. For instance, male hamsters that engage in more than five ejaculatory series sire more offspring by that female than do other males that may mate with her later. If the first male does not achieve at least five ejaculations, the second male will have equal or even greater reproductive success than the first male. Thus, the probability of a female copulating with more than one male while she is receptive may explain why species differ with respect to number of ejaculations.

Taken together, observations such as the ones above suggest that female reproductive physiology exerts considerable pressure on males to copulate properly. If he does not mount and dismount on the proper schedule, if he thrusts too many times or not enough times, or if he does not ejaculate often enough, his sperm will not fertilize as many eggs (or none at all) as they would if he had done everything properly. In other words, what may be going on in mammals is a phenomenon known as **cryptic sexual selection**.

The main point of cryptic sexual selection is to emphasize that females can still choose among males even after copulation has taken place. ("Choose" is used here merely for convenience. We can not get inside the mind of a peahen or rat, but we can observe that some males fail to father offspring (or father fewer than one might expect) even after they have copulated, so in a sense, females may be choosing internally even after they have chosen in a more obvious way.) For example, are female hamsters exerting a choice on males by "requiring" at least four ejaculations before conception can take place? Perhaps males that are not vigorous enough can not perform at that level. If he can not maintain the necessary timing of mounts and ejaculations, maybe he is not good enough for her to risk investing the considerable amounts of time and energy that are necessary to bring along a litter of pups. Maybe females just can not tell enough about male quality to make these choices and need this final performance evaluation before they make this big commitment. To summarize briefly, the great variability in the copulatory patterns and quantitative variations on those patterns that exist among mammals may be due to cryptic sexual selection exerted by females. Ovulation may not be triggered or fertilized eggs may not implant into the uterine wall unless the male copulates properly. Or the female may avoid using the sperm of males that do not copulate properly. These are fascinating possibilities that are just now beginning to be explored.

Excessive Sex by Females

Another type of quantitative difference in copulation is just beginning to receive attention. Females may copulate more often with one male or may copulate with more males than would seem to be necessary to become fertilized. After all, why would more than one copulation be needed when millions of sperm can be released in each ejaculation? One possibility is that extra copulations by females may be advantageous because the male with whom a female copulates may be temporarily low on sperm because of previous copulations, and because many sperm are defective or have low motility.

Another hypothesis is that males are more tolerant toward young who are born to females with whom they have copulated. In essence, if a male **could** be the father, he does not mistreat the young. Females who copulate with multiple males may gain by switching off the offspring-destructive tendencies of some males. Both these ideas may, of course, be true of some species but not others. More information will need to be collected before these hypotheses can be thoroughly tested.

Other Functions of Copulation

The relationship between copulatory behavior patterns and female reproductive physiology should suggest that the function of copulation is not solely to place sperm into the female reproductive tract. Let's review some additional functions.

Mate Recognition

A fascinating and apparently unusual effect of copulation is to activate an olfactory recognition system in the female. Female mice that had just been mated were placed alone in a cage that contained the odor of a male of the same strain as the stud, or the odor of a different strain. The female was left there for forty-eight hours and then moved to another cage that housed the stud or a male of the other strain. Pregnancy blockage occurred in those females that were placed with a male of the strain other than the one to whose odor they had been exposed after mating. Usually this would be the stud male and the appearance of a stranger male would induce the pregnancy block. Early curtailment of pregnancy under such circumstances is adaptive to the female because the "new" male will most likely kill her pups. Males are far less likely to kill a female's offspring if they have recently mated with her.

Male Parental Investment

In addition to sperm, males sometimes contribute other substances of reproductive consequence. For example, spermatophores (packets of sperm) of male butterflies contain nutrients that appear in the female's eggs. The same is true in the Mormon cricket. Copulation in these species is not only a sexual act, but a parental one as well.

Reducing Reproductive Competition

Female reproductive output is a resource for which males compete. Males who succeed, by whatever means, in acquiring more than an average amount of reproductive success will leave copies of those genes that contributed to that success. Competition for females may occur before mating takes place, a familiar phenomenon, but it may also occur during copulation itself. There are several ways that this may work.

First, copulation in some species involves the male removing sperm that may already be present in the female. In some damselflies (related to dragonflies) the penis is shaped in a way that allows the male to "rake" out sperm from the female's sperm-storage pouches. The last male to copulate with a female has the advantage, and males often guard females following copulation to prevent other males from removing their sperm.

Second, male semen may harden in the female's reproductive tract, forming a plug that impedes the movement of sperm of males who may copulate later with that female. These plugs have been found in snakes, ground squirrels, and other species.

Finally, males may deposit a pheromone (a chemical communication signal) that has an "anti-aphrodisiac" effect on other males. This appears to be the case in garter snakes, some moths, and others.

In conclusion, copulation often does much more than merely get sperm and eggs together. These additional functions may set the selective conditions favoring one copulatory pattern over another, or some quantitative variant over another. Perhaps these functions, which are not widely understood, will provide the keys to understanding the variety that exists in the copulatory patterns of mammals.