9.10 Male Reproductive Physiology

Learning Objectives

- List the phases of mitosis in order with brief descriptions of the events in each phase
- Explain how meiosis differs from mitosis
- Explain the differences in chromosome handling in meiosis I and meiosis II divisions
- Explain the origin of the genetic differences among germ cells
- Trace the path of sperm from testes to urethra during ejaculation
- Identify the major parts of a spermatozoa
- Identify the major sex accessory glands in the human
- Define GnRH and indicate its site of origin
- Describe the chemical nature of LH and FSH and indicate their cells of origin
- Identify the major targets of LH and FSH in males
- Describe the nervous control of erection in males
- Describe the nervous control of ejaculation

SOMATIC CELLS DIVIDE BY *MITOSIS*; GERM CELLS DIVIDE BY *MEIOSIS*

Humans have in general two types of cells: the **somatic** cells make up the vast majority of the cells and are the body cells. These cells grow and divide by **mitosis**. The second type of cell is the **germ cell**, which is used solely for reproduction and derives from somatic cells by a special kind of cell division called **meiosis**.

Long threads of double-stranded DNA make up the genetic material of all cells, and this material is organized into compact units called **chromosomes**. "Chromosome" literally means "colored body" and refers to the ability of these structures to stain with particular dyes that enables visualization under the microscope. Each chromosome consists of a single long piece of double-stranded DNA that is complexed with a variety of proteins that organize its structure and regulate the transcription of the DNA. The organization of the chromosomes varies depending on the stage of the cell's cycle. Chromosomes are most visible and most compact during cell division.

Each chromosome in the somatic cell is part of a homologous pair. These are two versions of the chromosome that have similar but generally not identical DNA sequences. The double-stranded DNA in each chromosome consists of a number of genes. **The gene is *defined* as the unit of inheritance**. Each gene consists of a sequence of nucleotides that carries the instructions for the synthesis of a protein that has some function. Because the chromosomes are paired, nearly every gene also comes in pairs, one on each chromosome. However, the two genes often differ in tiny details. These alternate forms of the genes in a single person are called **alleles**. The complete set of alleles of a particular person is that person's **genotype**. The set of proteins and other materials that the person actually makes, and which determines their outward appearance and behavior, is called the **phenotype**. Humans have 23 pairs of chromosomes. Twenty-two of these pairs are called **autosomes** which are common to all persons. The last pair of chromosomes are the sex chromosomes that are distributed differently in men and women. The sex chromosomes are grossly unequal, and some of the genes on the sex chromosomes are not paired.

MITOSIS PRODUCES TWO DAUGHTER CELLS WITH THE SAME DNA CONTENT AS THE ORIGINAL CELL

Because each somatic cell has two genes for nearly every trait, the condition is called **diploid** (2*N*). During development, cells grow and divide by mitosis so that each daughter cell also contains the full genetic complement of paired alleles. This process of cell division is summarized in Figure 9.10.1. The entire process is the cell cycle, which is under complex control. During **interphase**, the cell acquires more material and enlarges. It duplicates its DNA and the **centrosome**. The duplicate DNA condense during **prophase** forming **sister chromatids** that remain attached to each other. At this stage, there are four copies of each gene, two of each allele. However, the genes are not active at this time; in the condensed state, they are not being used to make mRNA which codes for the synthesis of new proteins. The centrosome consists of two centrioles oriented at right angles and a centrosome matrix that contains many copies of γTuRC (γ tubulin ring complex) which provides nucleation sites for microtubule assembly. During prophase, the **mitotic spindle**

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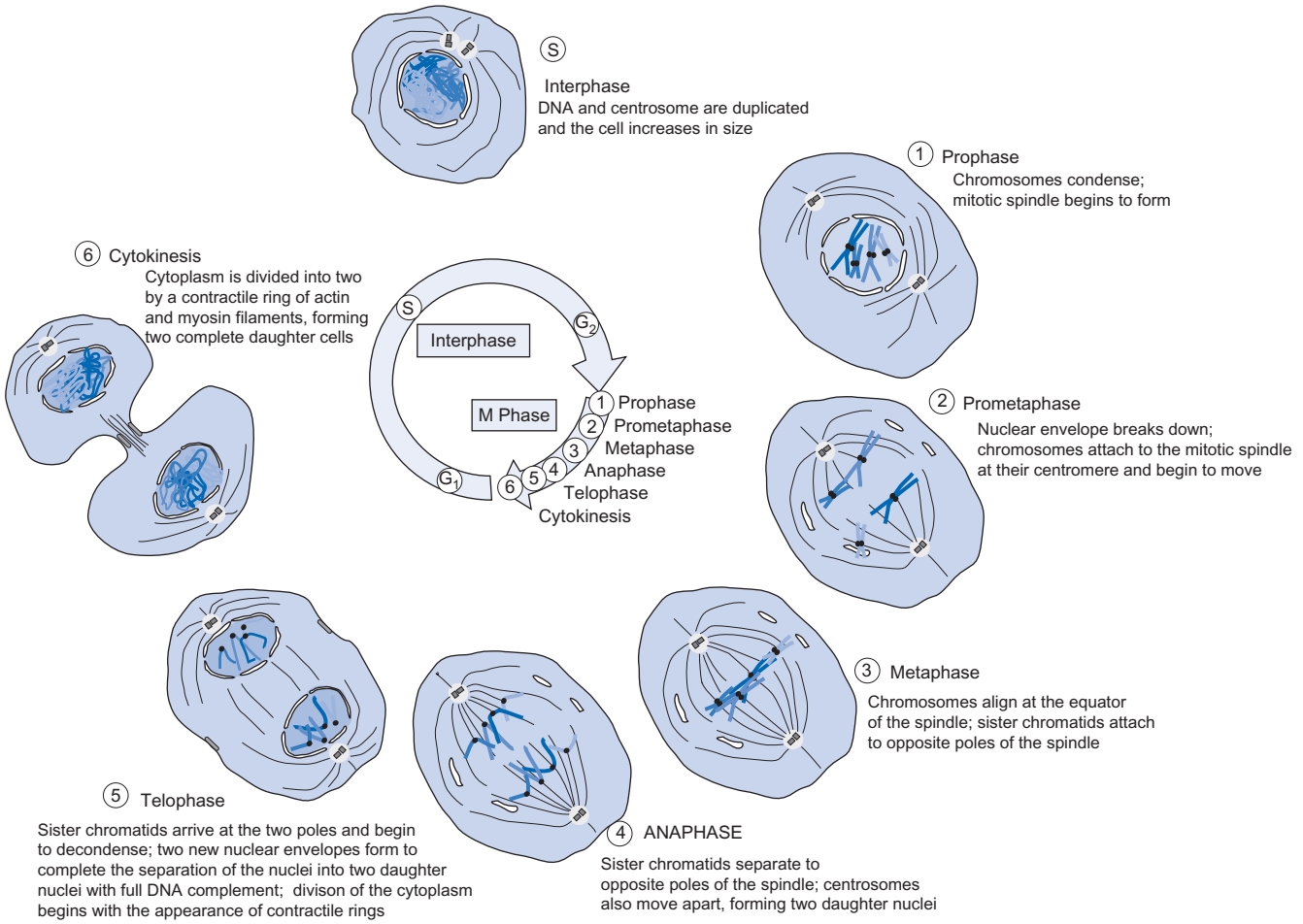

FIGURE 9.10.1 Mitotic cell division. During the synthetic part of interphase, S, the DNA of the chromosomes is duplicated to form identical sister chromatids for each chromosome. The centrosomes are also duplicated. In prophase, the chromosomes condense and the mitotic spindle begins to form. In prometaphase, the nuclear envelope disappears and the chromosomes attach themselves to the mitotic spindle at their kinetochore and begin to move. At metaphase, all of the chromosomes line up at the equator of the mitotic spindle. In anaphase, the sister chromatids separate to opposite poles of the mitotic spindle and the centrosomes move apart. During telophase, the nuclear envelope forms again, making two distinct daughter nuclei. The cell division is completed by separation of the cytoplasm into two daughter cells by constriction of the surface membrane by a contractile ring of cytoskeletal filaments. For clarity, only two homologous pairs of chromosomes are shown.

begins to form. The two centrosomes migrate toward opposite ends of the cell and form a complex arrangement of microtubules that provide tracks along which the chromosomes can move. This movement separates the chromosomes into two groups, but it occurs later, in anaphase.

In the next step, **prometaphase**, the nuclear envelope breaks down and the chromosomes attach to the microtubules of the mitotic spindle. In **metaphase**, the chromosomes align themselves along the equator of the spindle midway between the two centrosomes. They attach to the microtubules at the **kinetochore**. The kinetochore consists of a number of proteins that bind to a central part of the DNA called the centromere. Figure 9.10.2 illustrates the gross structure of a mitotic chromosome.

In **anaphase**, the sister chromatids separate to the opposite poles of the mitotic spindle. Cells have a mechanism that detects unattached kinetochores, so that anaphase does not occur until all of the chromosomes

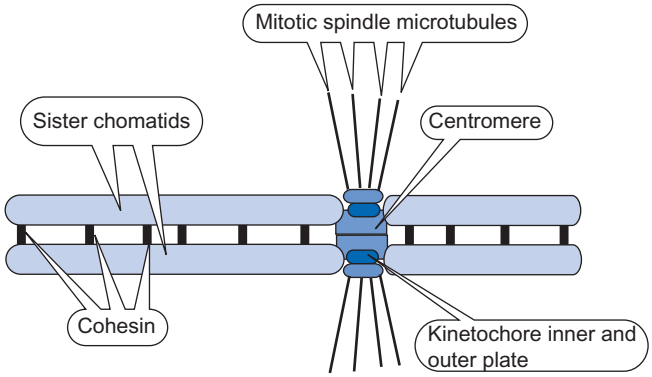

FIGURE 9.10.2 Simplified structure of the mitotic chromosome. The DNA of the chromosome has been duplicated and then condensed to make two sister chromatids that are identical in nearly all respects. They are linked along their length by the protein cohesin. A central region of DNA, the centromere, binds a set of proteins that form the kinetochore, which in turn anchors the microtubules of the mitotic spindle. During anaphase, the sister chromatids are separated by proteolytic cleavage of the cohesin and movement of the sister chromatids in opposite directions along the microtubule tracks provided by the spindle.

are attached and located at the equator of the spindle. Anaphase then begins with the activation of an anaphase promoting complex that has several functions. One is to activate a protease that clips the protein cohesin that glues the two sister chromatids together. When this is accomplished, the two sister chromatids can separate into the opposite poles of the mitotic spindle.

In **telophase**, a new nuclear envelope forms around the newly separated sister chromatids, which now form full chromosomes. They begin to decondense. This ends nuclear division, which is called mitosis or karyokinesis. The division of the cytoplasm, to separate the organelles of the cell into the component daughter cells, is called **cytokinesis**. It begins with a contractile ring that encircles the cell approximately midway between the two centrosomes. The contractile ring consists of actin and myosin filaments and its contraction squeezes the cell so that the cytoplasm is divided into the two daughter cells.

MEIOSIS DIVIDES THE PARENT GENOME IN HALF—BUT CROSSING-OVER DIVERSIFIES THE RESULT

Sexual reproduction in humans produces a single fertilized cell that grows and divides by mitosis. Eventually, through complex developmental events, the single fertilized cell becomes a baby, and eventually an adult. The fertilized cell is diploid, containing 23 pairs of chromosomes. Therefore, all of the cells it produces from mitosis also contain 23 pairs of chromosomes. The fertilized cell arises from fertilization of the **ovum**, produced by the mother, and a **spermatozoon** produced by the father. The 23 pairs of chromosomes results from the fusion of 23 chromosomes in the ovum with 23 chromosomes in the spermatozoon. The ova and sperm cells are collectively called **gametes**, or **germ cells**. They contain only half of the genetic complement of each parent and are called **haploid** (N). The process that produces these haploid cells is called **meiosis**.

Meiosis begins with the duplication of the full DNA complement of the cell to produce two sister chromatids for each chromosome, just as occurs in mitosis. In the first meiotic prophase, homologous chromosomes pair up to form a structure called a **bivalent**. This first meiotic prophase takes days and sometimes years. An extremely important event occurs in this bivalent, i.e., **crossing-over** of genetic material. This scrambles the genome and allows us to confidently assert that every human, save identical twins, is genetically distinct.

Division I of meiosis separates the homologous chromosomes, not the sister chromatids, along the spindle, so that each daughter cell receives one of each homologous pair of chromosomes. This produces two haploid daughter cells that still have two copies of each gene. Thus, these cells have a haploid number of chromosomes but a diploid amount of DNA. The sister chromatids are identical except where genetic recombination, crossing-over, has occurred. The daughter cells produced by meiosis I then undergo a second meiotic division to separate the sister chromatids. The process of meiosis for the generation of spermatozoa is illustrated in Figure 9.10.3.

REASSORTMENT OF GENETIC MATERIAL ARISES FROM TWO SOURCES: INDEPENDENCE OF HOMOLOGOUS CHROMOSOME SORTING AND CROSSING-OVER

As shown in Figure 9.10.3, each somatic cell contains pairs of homologous chromosomes, one-half contributed by the father and the other half contributed by the mother. In the meiotic divisions that produce the gametes, the first meiotic division separates the homologous pairs from each other. These homologous pairs are separated randomly. Since there are two ways to sort each member of a single pair, and the sorting is independent, the number of possible combinations of the maternal and paternal homologs in the final gamete is 2^N, where N is the number of chromosomes in the haploid state, or the number of pairs of chromosomes in the diploid state. Since in humans $N = 23$, the number of possible combinations of maternal and paternal homologous chromosomes is $2^{23} = 8.4 \times 10^6$.

The actual number of unique combinations of genes in the germ cells is actually much greater than this because there is a second source of reassortment of genes in the spermatogonia called crossing-over. In the long prophase of meiosis I, in which the two homologous chromosomes are in close contact, parts of the homologous chromosomes exchange with each other. On average, two or three crossover events occur in each chromosome during this stage. How this produces a large number of unique germ cells is illustrated in Figure 9.10.4. Briefly, each crossover in a given primary spermatocyte will produce four possible arrangements of the sister chromatids. But the number of possible crossovers is much greater. Thus, in one primary spermatocyte the crossover may occur between an extreme end of the chromosome and produce four unique sister chromatids; in another the crossover may occur in a different place. Thus, the number of unique combinations of genetic information from one parent is large.

The production of gametes or germ cells occurs in both males and females, but there are significant differences between them. The above discussion describes both processes in general but its emphasis is on the production of sperm, as shown in Figure 9.10.3. The purpose of the sperm, of course, is to combine genetic information with that of the ovum during the process of fertilization. All of the structures associated with the male reproductive tract are evolved with the purpose of delivering sperm to the female so that the probability of fertilization is enhanced. A section of the male reproductive system is shown in Figure 9.10.5.

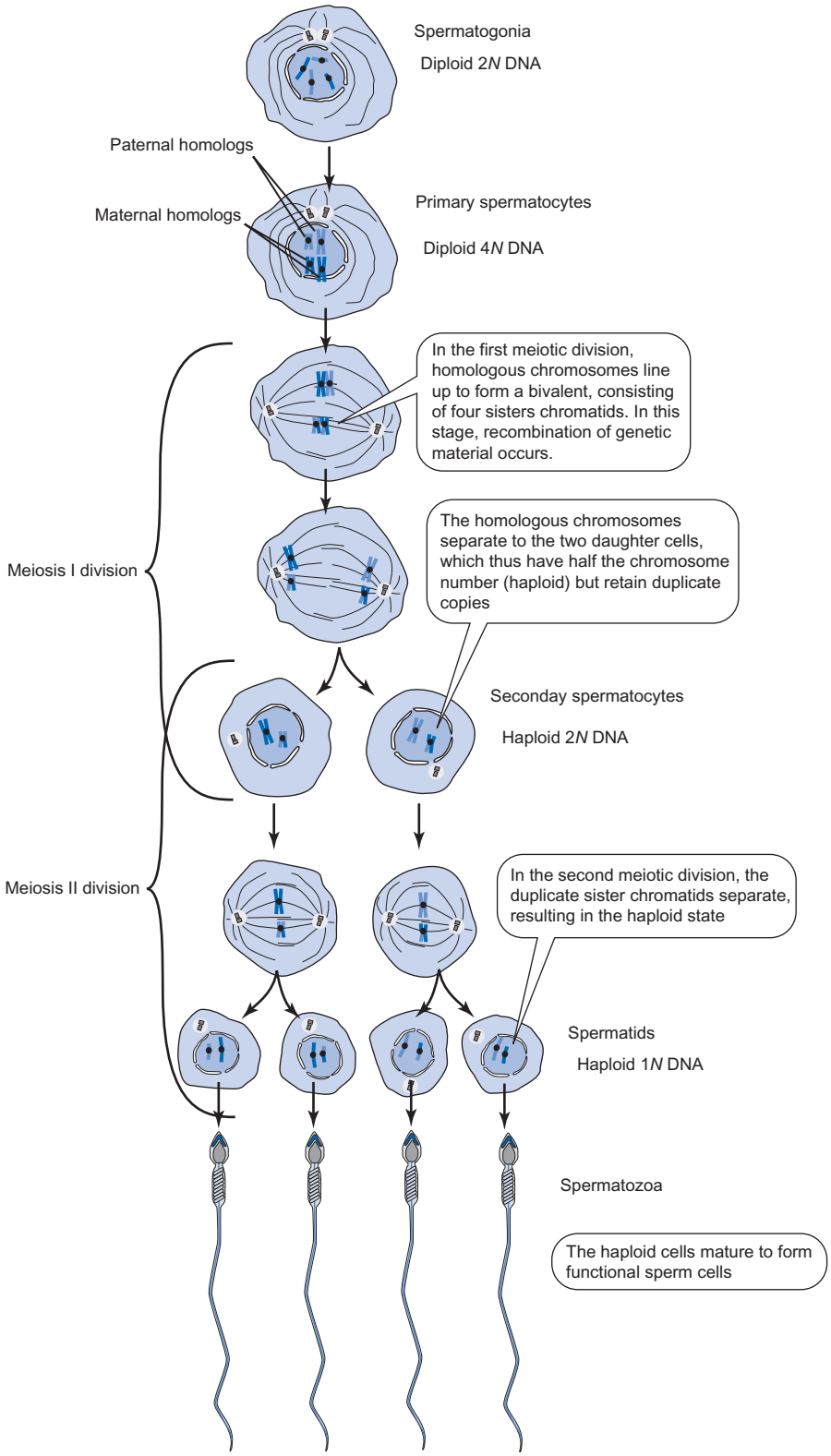

FIGURE 9.10.3 Meiosis in the production of spermatozoa. These cells continue to divide mitotically throughout adulthood. Some of the daughter cells become primary spermatocytes and undergo meiotic division, shown here. These primary spermatocytes are diploid cells with duplicated DNA, so they have 2*N* chromosomes and 4*N* DNA. In the first division, the duplicated homologous chromosomes are condensed and then aligned on the equator of the spindle in the form of a bivalent, consisting of four sister chromatids, two from each homologous pair of chromosomes. The homologous pairs separate randomly, one of each going to each daughter cell, which are called secondary spermatocytes. The secondary spermatocytes thus are haploid, with *N* chromosomes and 2*N* DNA. The chromosomes in the secondary spermatocyte are then aligned again on the spindle in the second meiotic division, and the sister chromatids are separated into the spermatids, which are haploid, with *N* chromosomes and 1*N* DNA. These spermatids then mature into spermatozoa.

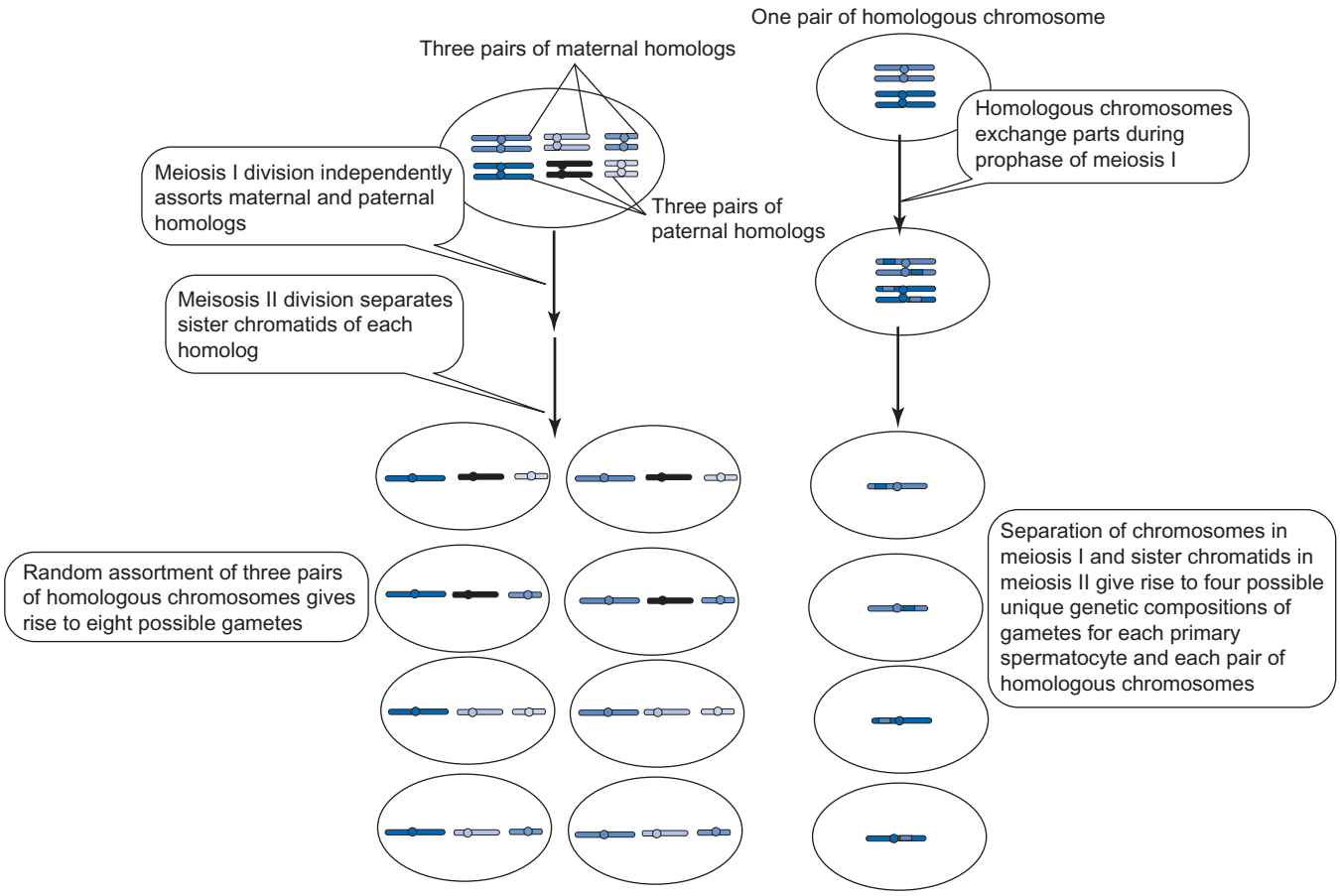

FIGURE 9.10.4 Origin of variation of the DNA content of germ cells. The adult somatic cells have paired chromosomes that contain different genetic information, some resulting from the mother (the set of maternal homologous chromosomes) and some resulting from the father (the set of paternal homologous chromosomes). This is the diploid number, 2*N*. During interphase, the chromosomes are duplicated to form sister chromatids and a diploid cell with 4*N* DNA. In meiosis I division, the homologous chromosomes are separated, creating haploid cells with 2*N* DNA. The sister chromatids are then separated in meiosis II, producing haploid cells with 1*N* DNA. Because meiosis I division randomly separates maternal and paternal homologs, there are multiple possible combinations of the final haploid germ cells. For *N* chromosomes, there are 2^N possible combinations. This genetic diversity is greatly enhanced by crossover between the maternal and paternal homologs in prophase of meiosis I. In this stage, the two homologous chromosomes with their sister chromatids are in close proximity, and parts of the maternal homolog on one sister chromatid may cross over to the paternal homolog and vice versa. This produces four nonidentical chromatids. For every crossover, there are four possible unique combinations of genes in the final haploid cells. Crossover can occur at a variety of points in the chromosome, so that the final number of possible germ cells is $2^N \times 4 \times$ the number of unique crossovers possible. *(Source: Adapted from B. Alberts et al.,* The Molecular Biology of the Cell, *2002.)*

TESTICLES PRODUCE SPERM AND TESTOSTERONE

TESTICLES REQUIRE LOWER TEMPERATURE FOR SPERM PRODUCTION

In man and most other mammals, the testicles reside in a pouch of skin called the **scrotum** that hangs outside of the body. This position lowers the temperature within the testicle some 1°C or 2°C. This lower temperature facilitates sperm production. A thin muscle called the cremaster muscle can retract the testicles toward the abdomen to increase their temperature when environmental temperatures are low and relax to extend the testicles when environmental temperatures are higher. Research suggests that the number of sperm produced by men today is less than that produced by men of former times, perhaps due to the wearing of tighter clothes and subsequent higher temperatures within the testicles.

TESTES PRODUCE SPERMATOZOA

Spermatozoa are produced within structures called the **seminiferous tubules**. These tubules contain stem cells called **spermatogonia** (singular is spermatogonium) that derive from primordial germ cells that enter the testis during embryogenesis. The spermatogonia reside near the basement membrane of the stratified epithelium of the seminiferous tubules, as shown in Figure 9.10.6. After the onset of puberty, and continuing throughout adult life, these spermatogonia divide mitotically and some of them enter the first meiotic division to form **primary spermatocytes**. These are diploid, having 2*N* chromosomes, with duplicate sister chromatids for 4*N* DNA. These primary spermatocytes separate the pairs of homologous chromosomes in the first meiotic division to become **secondary spermatocytes**, which are haploid (1*N*) with 2*N* DNA. The spermatocytes then undergo meiosis

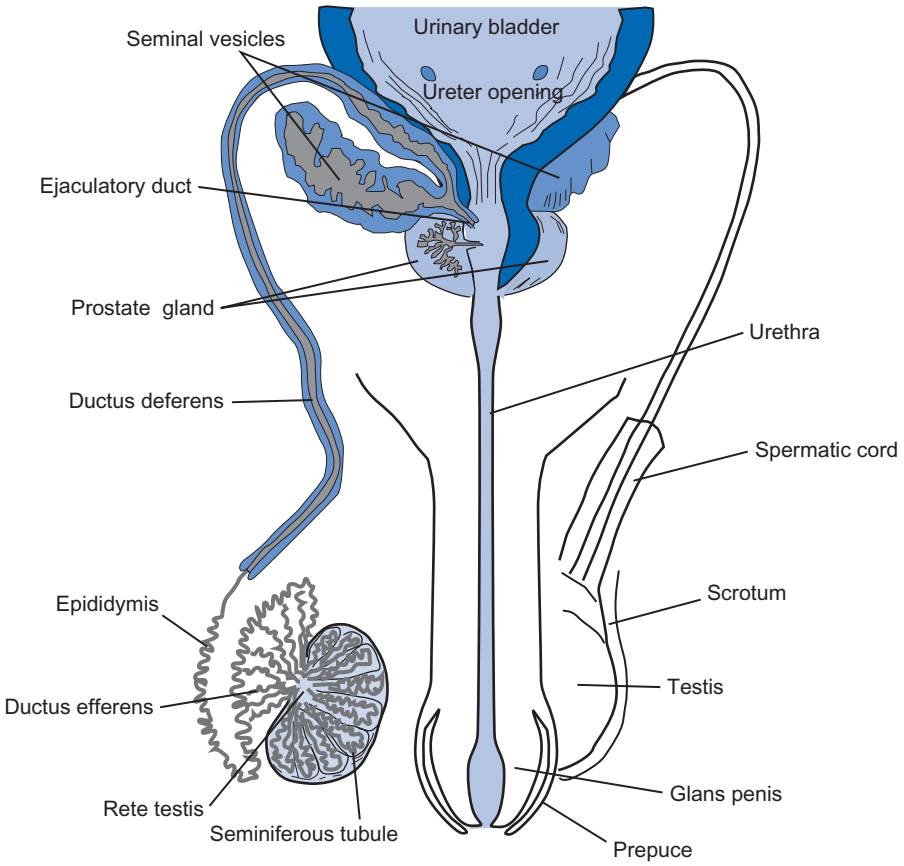

FIGURE 9.10.5 Anatomy of the male reproductive system. Sperm is produced in the seminiferous tubules, then traversing in succession the rete testis, ductuli efferentes, epididymis, vas (ductus) deferens, ejaculatory duct, and the urethra.

II in which the sister chromatids separate into the spermatid cells. Each primary spermatocyte gives rise to two secondary spermatocytes, and each of the two secondary spermatocytes gives rise to two **spermatids**.

Spermatids transform into spermatozoa in a process called **spermiogenesis**. This involves reduction of the volume of cytoplasm and formation of the specialized parts of the spermatozoa. Figure 9.10.7 shows a mature spermatozoon, also called a sperm cell.

The **Sertoli cells** (see Figure 9.10.6) provide nutrients and support for the formation and maturation of spermatids. These cells are large, polyhedral-shaped cells that extend from the basement membrane of the seminiferous tubules to the lumen. Extensions of the Sertoli cell cytoplasm surround the spermatids during the early stages of spermiogenesis. Eventually the maturing spermatids are released from the Sertoli cells in a process called spermiation.

Spermatogenesis is not random. Groups of spermatogonia are often in step and groups of them will initiate a cycle of development about every 16 days. Throughout the testes, these groups are not synchronized so that overall there is a continuous production of spermatozoa. The whole of spermatogenesis from spermatogonia to spermatozoa takes approximately 74 days (Figure 9.10.8).

THE TESTES MAKE TESTOSTERONE

The second main function of the testes is to make testosterone. Testosterone is made by the **Leydig cells**, which are interstitial cells interspersed among the seminiferous tubules. The biochemical pathways leading to the synthesis of various androgens is shown in Figure 9.10.9. Some of these reactions are not predominant in the Leydig cells themselves, but occur in target tissues. Notable among these is the conversion of testosterone to dihydrotestosterone by the **5α reductase** enzyme. This reaction typically occurs in target tissues of testosterone, not in the Leydig cells.

THE HYPOTHALAMUS AND ANTERIOR PITUITARY CONTROL TESTICULAR FUNCTION

CELLS IN THE HYPOTHALAMUS SECRETE GONADOTROPIN-RELEASING HORMONE

Neurons that synthesize and release GnRH, gonadotropin-releasing hormone, are dispersed throughout the hypothalamus but are believed to be concentrated in the arcuate nucleus and preoptic area. These cells synthesize GnRH as a precursor preprohormone containing 92 amino acids. Cleavage of the signal sequence releases a 69-amino-acid prohormone which is again cleaved to form a 10-amino-acid fragment which is the active GnRH. When stimulated, these neurons release GnRH into the hypothalamic portal circulation, which then travels to the anterior pituitary gland where the GnRH stimulates gonadotrophs to release follicle stimulating hormone (FSH) and luteinizing hormone (LH) into the general circulation. GnRH increases LH and FSH release by activating a

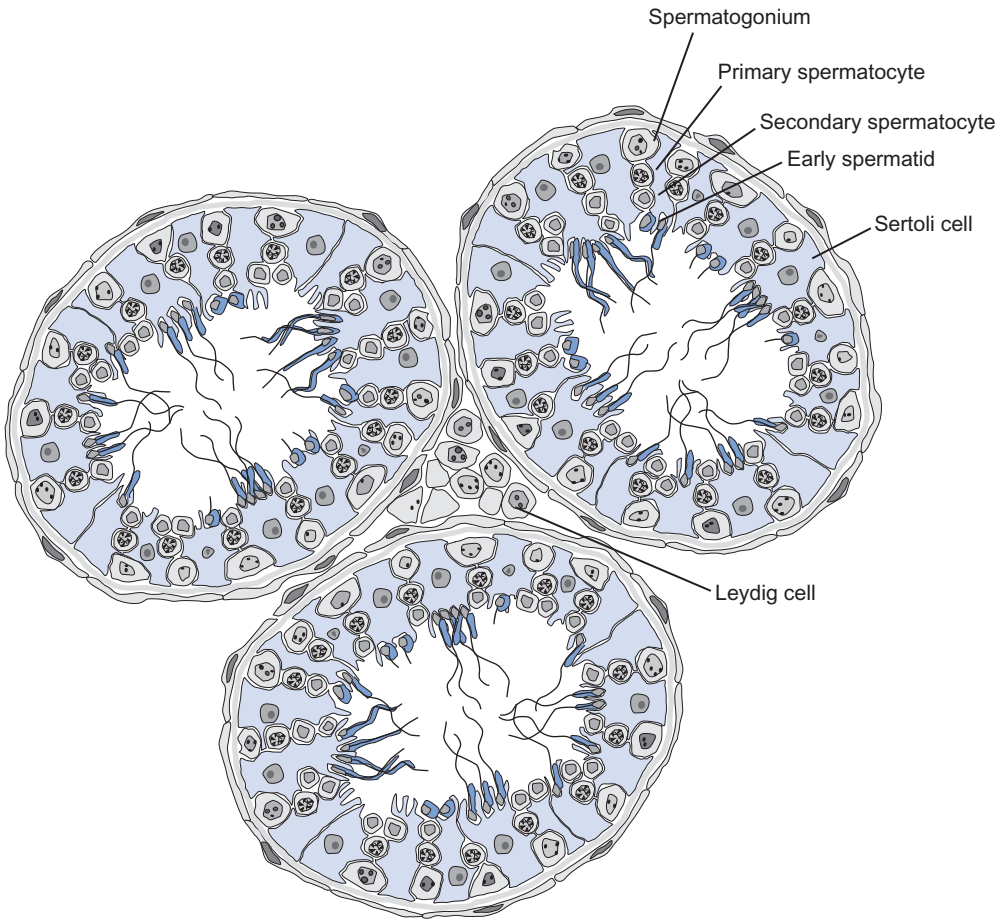

FIGURE 9.10.6 Seminiferous tubules. Spermatogonia cells lie near the outer rim of the tubules adjacent to the basement membrane. They continuously divide by mitosis to form additional spermatogonia. Some spermatogonia become primary spermatocytes, which undergo crossing-over in the prophase to the meiosis I division. After meiosis I division, the daughter cells are called secondary spermatocytes and these cells are haploid. The secondary spermatocytes undergo a second meiotic division to form the spermatids. These then undergo spermiogenesis to transform into spermatozoa.

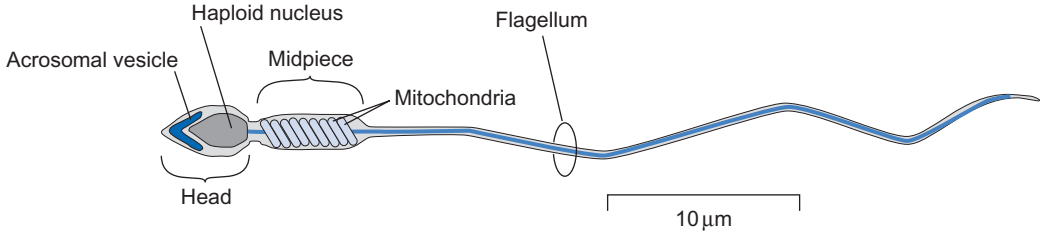

FIGURE 9.10.7 Mature spermatozoon. The genetic information is packaged in a tight bundle in the haploid nucleus in the head region. Surrounding it is an acrosomal vesicle that helps the sperm penetrate the ovum. The spermatozoa's motility derives from its flagellum, which is powered by a group of mitochondria in the midpiece.

G_q mechanism in which the α subunit of the heterotrimeric G protein activates phospholipase C, which hydrolyzes membrane phosphatidyl inositol bisphosphate to liberate IP3 and diacylglycerol (DAG). The released IP3 binds to IP3 receptors on the endoplasmic reticulum membrane and causes Ca^{2+} release from the ER stores; the released DAG activates protein kinase C (PKC). The net effect of GnRH binding to the gonadotrophs is increased synthesis and release of FSH and LH.

CONTROL OF GnRH SECRETION IS STILL INCOMPLETELY UNDERSTOOD

The exact mechanisms responsible for GnRH release are not known in detail. It is known that GnRH release is pulsatile, and therefore the release of LH and FSH from the anterior pituitary is also pulsatile. This pulsatile release is absolutely essential: continuous release of GnRH produces a downregulation of their receptors

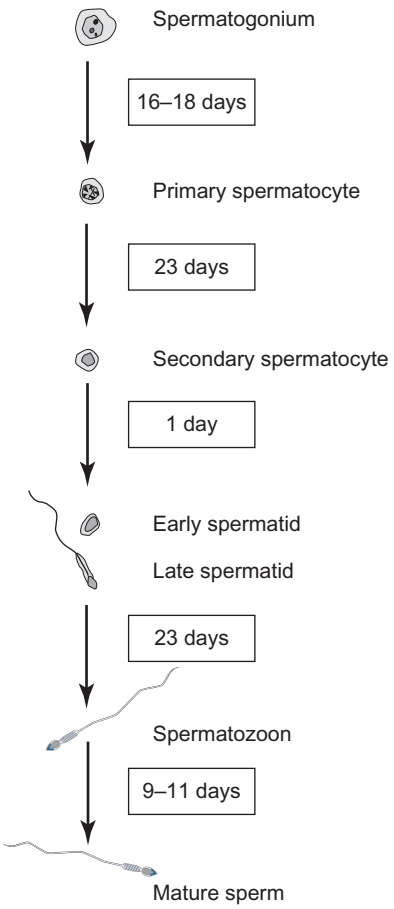

FIGURE 9.10.8 Development of sperm. Each of the stages that make up spermatogenesis has its own specific duration; the spermatogonia take 16–18 days to form the primary spermatocytes; the primary spermatocytes take 23 days to make the secondary spermatocytes; the secondary spermatocytes take only one day to become spermatids, and the spermatids spend another 23 days maturing into spermatozoa. This does not add up to 74 days because after release of the spermatozoa into the lumen of the seminiferous tubules, the spermatozoa still require maturation. The released spermatozoa are not yet motile, and they are transferred to the rete testis and epididymis by movement of the luminal fluid, not by motility of the sperm. In the epididymis, the spermatozoon undergoes maturation processes that progressively enable it to bind to the zona pellucida of the ovum and to fertilize the ovum.

and subsequent reduction in LH and FSH release. Secretion of GnRH is inhibited by circulating levels of testosterone.

BOTH LH AND FSH CONTROL TESTICULAR FUNCTION

LH AND FSH ARE GLYCOPROTEINS THAT BELONG TO THE SAME FAMILY AS TSH AND HUMAN CHORIONIC GONADOTROPIN

Human chorionic gonadotropin (hCG), thyroid-stimulating hormone (TSH), FSH, and LH are all glycoproteins composed of an α and a β chain. All four of these hormones have identical α chains consisting of a 92-amino-acid sequence. Thus, the β chain confers specificity of action.

LH STIMULATES LEYDIG CELLS TO PRODUCE TESTOSTERONE

Although LH derives its name (luteinizing hormone) from its effects on the female reproductive system, it also has important effects in the male. Leydig cells have receptors for LH on their surface membranes that operate through a G_s mechanism. The increased cAMP levels result in increased synthesis and subsequent activity of a number of enzymes involved in the synthesis and secretion of testosterone. The mechanisms for this activation are similar to those of ACTH on adrenal steroid synthesis (Figure 9.5.6). Some 95% of the circulating testosterone originates from the Leydig cells of the testes.

TESTOSTERONE HAS LOCAL AND SYSTEMIC EFFECTS

Testosterone released from the Leydig cells appears in the general circulation and also has local effects on the Sertoli cells that reside just a few hundred microns away from the Leydig cells. Sertoli cells contain **androgen binding protein** (ABP) that binds testosterone and is secreted into the seminiferous tubules. Presumably this presents high concentrations of testosterone to the developing spermatozoa so as to maintain spermatogenesis. Testosterone exerts multiple effects including:

- Maintenance of spermatogenesis in seminiferous tubules and maturation of spermatozoa in the epididymis.
- Maintenance of size and function of the accessory sexual organs.
- Development of secondary sex characteristics at puberty and maintenance postpuberty:
  - size of external genitalia;
  - laryngeal enlargement leading to deepening of the voice;
  - secretion of sebaceous glands, tending toward acne;
  - masculine pattern of muscle mass and anabolism;
  - male hair distribution.
- Behavioral effects: increased libido and aggressiveness.
- Pubertal growth spurt.

FSH STIMULATES SERTOLI CELLS TO PRODUCE A NUMBER OF PROTEINS

Sertoli cells have receptors for FSH on their surface membranes that are linked to a G_s mechanism. The resulting increase in cAMP alters the expression of some 100 proteins. Important among these are the following:

- Increasing aromatase: this enzyme converts testosterone to estradiol or androstenedione to estrone.
- Increasing **ABP**.
- Increasing **inhibin**, a protein that feeds back onto the anterior hypothalamus to shut off gonadotroph secretion.
- Increasing growth factors that support spermatogenesis.

The feedback regulation of GnRH, LH, and FSH secretion is shown in Figure 9.10.10.

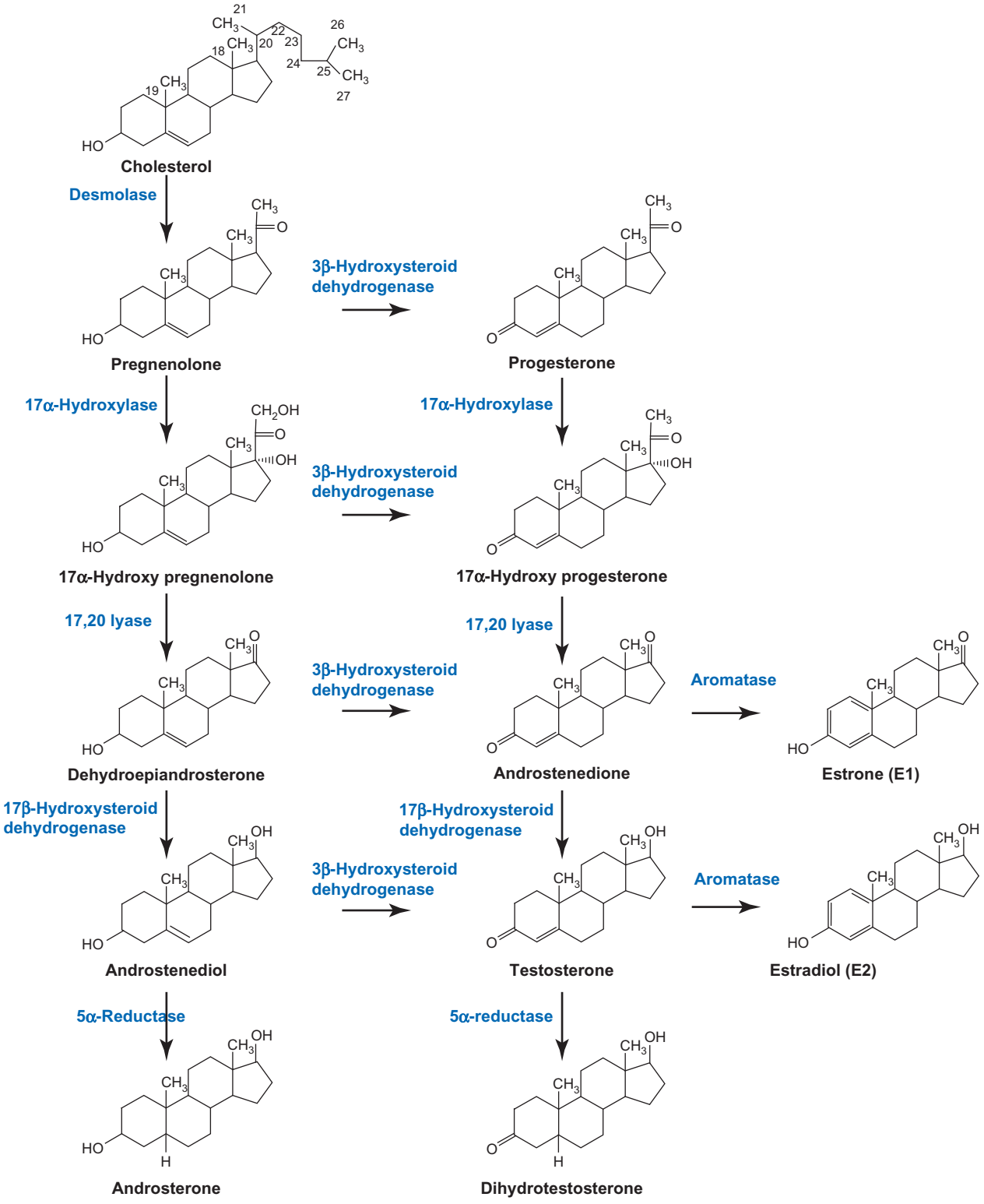

FIGURE 9.10.9 Pathway of androgen synthesis in Leydig cells and androgen metabolism in target cells. Testosterone is synthesized and secreted by the Leydig cells and conversion to dihydrotestosterone generally occurs in the target tissues.

THE MALE SEXUAL RESPONSE

The sexual response consists of four phases:

1. Arousal or excitement phase
2. Plateau phase
3. Orgasmic phase
4. Resolution phase or refractory period.

All of these phases involve the autonomic nervous system, integrated with higher order functions. The most important sexual organ is the brain. Mechanical

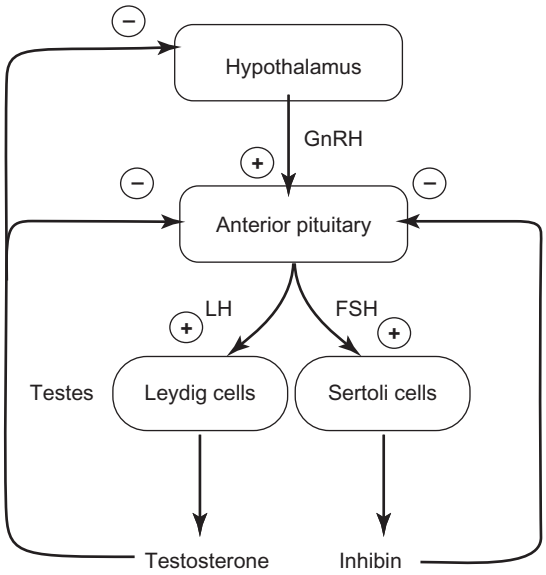

FIGURE 9.10.10 Feedback regulation of GnRH, LH and FSH secretion in the male.

stimulation of the penis or expectation of sexual interactions produces the excitement phase, which in the male is the **erection** of the penis in preparation for sexual intercourse. Penile erection results from a complex interaction of psychological, neural, vascular, and endocrine factors and is usually, but not exclusively, associated with sexual arousal. Penile erection can also occur in response to a full urinary bladder or during rapid eye movement sleep.

Penile erection results from engorgement of the **corpus cavernosa** with blood. The corpus cavernosa are two tubular structures running the length of the penis. Thus, it is ultimately the blood pressure that enables the hardening and enlargement of the penis during erection. Parasympathetic nerves supplying the vessels release NO, nitric oxide, from nerve endings and endothelial cells. The NO activates guanylate cylcase to increase levels of cGMP in the tissue. This relaxes the vascular smooth muscle, as described in Chapter 3.8. Drugs such as sildenafil (viagara) act by inhibiting cGMP phosphodiesterase, preventing cGMP breakdown. These drugs cannot act without parasympathetic activation of erection.

Ejaculation, the emission of semen from the penis, is mediated by sympathetic nerves. The normal volume of the ejaculate is 3–4 mL consisting of spermatozoa and the seminal plasma made up of the secretions of the testes and accessory sex organs including seminal vesicles, prostate gland, and bulbourethral gland. The seminal vesicles contribute 65–75% of the semen volume; the prostate contributes 25–30%, and about 5% is contributed by the testes. The semen is a white opalescent fluid that coagulates after ejaculation. The seminal vesicles add a protein, **semenogelin**, to the ejaculate and this protein causes the coagulation reaction after mixing with prostate fluid. Semenogelin is the major protein in the seminal plasma. After 10–20 min, the semen liquefies again due to proteolysis of the semenogelin by **prostate specific antigen (PSA)**, which is a protease added to the semen by the prostate gland. The seminal vesicle also adds **fructose** to the semen, in excess of 100 mg%, which is the predominant energy source available to the sperm. The ejaculate typically contains 1×10^8 sperm mL^{-1}. Values below 20×10^6 sperm mL^{-1} are considered insufficient for fertilization.

SUMMARY

Cell division in the somatic, or body, cells is called mitosis and consists of an elaborate mechanism for duplication and separation of the entire genome. Duplication occurs during interphase. In prophase, the chromosomes condense and the mitotic spindle forms. In metaphase, the nuclear envelope breaks down and chromosomes align along the equator, bound to the spindle at their kinetochore. In anaphase, the sister chromatids separate to opposite poles. In telophase, division of the cell cytoplasm occurs, the nuclear membrane reforms, and the chromosomes decondense.

Formation of the gametes, or sex cells, requires meiosis. In this case, the pairs or chromosomes duplicate, producing four sequences for each gene: the original and a copy of each of two alleles or alternate forms of a gene found on homologous chromosomes. In meiosis I, homologous chromosomes separate randomly, so that many different combinations of genes are possible. In meiosis II, the sister chromatids separate, producing the haploid (N) gametes. Parts of homologous chromosomes can also cross over or exchange material between homologous chromosomes. This process greatly increases the number of possible rearrangements of the genes in the germ cells.

The male sexual organs consist of the testicles, penis, and accessory organs consisting of a pair of seminal vesicles, a single prostate gland, and a bulbourethral gland. The paired testes produce sperm and testosterone. These testes are suspended outside the body in the scrotum, as the sperm require a slightly lower temperature for maturation. The penis is a delivery system for the sperm to the female's vagina. Spermatogenesis occurs in the seminiferous tubules, requiring 74 days for completion to mature, motile spermatozoa, with final maturation in the epididymis. This process is regulated by FSH and testosterone. Leydig cells in between the seminiferous tubules synthesize testosterone under stimulation by LH. FSH increases synthesis of ABP and inhibin by the Sertoli cells that nourish the developing sperm. Testosterone inhibits LH release from the anterior pituitary; inhibin inhibits FSH release.

Circulating testosterone promotes development of secondary sex characteristics, masculine body type and behavior, and development and maintenance of the genitalia and accessory sex glands.

Vasodilation of vessels supplying the corpus cavernosa, and restriction of the outlet, produces penile erection. This is accomplished through parasympathetic release of NO. Ejaculation is controlled by the sympathetic nervous system. The ejaculate consists of 3–5 mL of fluid

originating from the testes (5%), seminal vesicles (70%), and prostate (25%). The ejaculate gels quickly due to semenogelin and then liquefies after 10–20 min from the action of PSA. This probably enables the sperm to stick to the vaginal walls.

REVIEW QUESTIONS

1. List the phases of mitosis in order. At which phase is DNA duplicated? When do the chromosomes condense? When do they line up at the equator? When do they separate? What part of the genotype separates in this phase of mitosis?
2. What is separated in meiosis I? How many ways can this occur? What is the composition of the separated chromosomes? What is separated in meiosis II?
3. What keeps sister chromatids together? What separates them? What is the centromere? What is the kinetochore?
4. Where are sperm made? Where do they mature? What hormones are necessary for their development?
5. What causes penile erection? What causes ejaculation?
6. Name the accessory sex glands. Which contributes the highest proportion of volume to the ejaculate? What contributes the least? What energy source is added to the ejaculate to support the sperm? What causes coagulation of the semen? What cause liquefaction of the semen? How many sperm does semen contain?
7. Where is GnRH synthesized? What cells release LH and FSH? What inhibits their release?
8. What cells does LH stimulate? What do they make in response? What cells does FSH stimulate? What do these cells do in response to FSH stimulation?