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ONE

Human reproductive strategies

It has been said that the final aim of all human love relationships between men and women is more important than all other ends in life, because what it determines is nothing less than the composition of the next generation. It is perhaps no coincidence, then, that reproduction – involving, as it does, sexual intercourse – has come to occupy such an important part of our lives. It is the driving force of evolution, and hence generates the great variety of living organisms which inhabit, and have inhabited, the Earth, including, of course, ourselves. However, notwithstanding the power of evolution, or perhaps because of the force of it, sex has come to mean much more to us than reproduction.

Normal sexual intercourse has been defined as anything erotic which gives pleasure to both partners, who are consenting adults, and does not hurt anyone. This clearly holds good for a wide variety of sexual functions within loving relationships. In this context, the word love should be taken to mean the desire for the good of the other person; wishing for gain, or to exercise power over another person does not occur in a loving relationship.

Clearly, there are not only emotional but also physical risks associated with having a sexual relationship. Unwanted pregnancies and sexually transmitted diseases can all too easily follow from unprotected sexual intercourse (see chapter 6 for more information about contraception). However, though it bears great personal responsibility and requires a degree of self discipline, sexual activity is normal and healthy and can be a joyous part of life.

Human beings are unique in the living world in that although we share with all other organisms an overwhelming drive to procreate, we are the only species consciously to limit the number of our offspring and to outlive, often by many years, our reproductive capacity. Like all other biologically based aspects of the human condition, the complex nature of human reproduction has come about in response to the various selection pressures to which it has been subjected. This is an underlying theme of this book, so it is appropriate, therefore, that we begin our study of human reproduction with a brief consideration of its evolution.

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1.1 An evolutionary perspective

Physiological adaptations

In evolutionary terms, reproduction is the most important defining characteristic of life (see also chapter 9). However, although it is vital for the survival of the species as a whole, it is not essential to the individual. Amongst living things there is an almost infinite variety of strategies for ensuring reproductive success, and humans are no exception to this. Human reproduction, though, is unique in two important respects: the extended period of development before sexual maturity is reached, and the lack of a defined mating season, or 'heat'.

In non-primate mammals, there is no **prepubertal** growth spurt: rodents, for example, become sexually mature whilst they are still growing. Primates, including humans of course, have a developmental mechanism which prevents the maturation of their **gonads** (ovaries and testes) until after they have undergone an increase in growth rate before adolescence. This provides an extended period for learning. Because they are small and relatively weak, the young can be more easily cared for, and they can learn through play without injuring each other too much. At **puberty** they quickly become much larger and stronger just as they mature sexually, so as they become adults they are capable of caring for their own smaller offspring.

In mature men the testes continually release **sperm** which is stored in the long, coiled duct of the epididymis. From time to time this is released via the vas deferens and mixed with secretions from the seminal vesicle and prostate gland to form seminal fluid, which is ejaculated from the penis during orgasm. Although there is no evidence that the central nervous system is made aware of the need for emptying of the epididymis or accessory glands, there is no doubt that the individual is fully cognisant of the special satisfaction of this event. In women, production of **oocytes** (ova or eggs) from the ovaries is cyclic, and involves no comparable accumulation of large numbers of gametes or quantities of fluid. However, the orgasm experienced by many woman is a sexual satisfaction comparable with that of male ejaculation, and has contributed to the heightened sexuality which is a particularly human characteristic. A detailed description of the functioning of the mature male and female reproductive tracts appears in chapters 2–5.

Humans are physiologically adapted for a frequent and repeated need for sexual stimulation and gratification. That sexual intercourse can take place at any time is an important factor in human social evolution. In contrast, mating episodes usually occur only around the time of ovulation in most other primates. In many of these species, such as the baboon and chimpanzee, changes indicating her receptivity to the male occur in the female external genitalia and behaviour. Human women, on the other

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hand, rarely experience any external sign that they are ovulating: occasionally there may be slight bleeding in the middle of the menstrual cycle, and although there is a slight rise in body temperature at the time of ovulation, the woman is rarely aware of it (chapter 7). There is no evidence that intercourse occurs more often at this time during the woman's cycle.

As **gametes**, sperm outnumber eggs by several orders of magnitude around the time of fertilisation. This means that sperm, from either one or several acts of intercourse with one or more partners, must compete with one another to fertilise the egg. This is a subject which has long been a source of fascination for reproductive and evolutionary biologists. Some suggest that this **sperm competition** may form the physical basis of much sexual behaviour between men and women. On a purely biological level, sperm competition takes place within each of the various strategies for human procreation: monogamy (having only one sexual partner at a time); serial monogamy (having more than one partner, but only one at a time); polygamy (having more than one female – or less usually male – partner at a time); and promiscuity (having several sexual partners at a time). Although it is the norm in Western society, not all human societies are monogamous, and in some the man takes little or no responsibility for raising children. This brings us to the question of whether the various observable physiological adaptations for reproduction may be linked to the human sexual behaviour which forms such an important part of our social life.

Social and behavioural adaptations

Just as anatomical and physiological adaptations are responses to evolutionary selection pressures, so behavioural patterns have evolved to help to ensure the reproductive success of our species. The study of the biological basis of social behaviour in animals, including humans, is called **sociobiology**, and it has helped to explain how the evolutionary pressures which have brought about all other survival adaptations have also played their part in the development of behaviour, including subtle examples related to reproduction, such as altruism, parent–offspring relationships, nepotism and sexism.

Although little detail is known, it is certain that fertility was a prevailing concern of people at the dawn of human evolution. Human courtship displays and reproductive strategies are the most complex and elaborate in the animal kingdom, and there seems little doubt that these patterns are based upon those of our early ancestors. While little is known of these, study of related species suggests that communication between the females and males which drew them together and promoted mating, and the reproductive strategy which ensured the efficiency of mating, were of fundamental importance.

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A characteristic of human sexual and mating behaviour is the formation of relatively long-lasting pair bonds. There is evidence that this also occurs in gibbons, but is not otherwise generally seen in primates. It is thought that during Pleistocene times, humans started to hunt in an organised way, and the men who went hunting probably spent extended periods away from the rest of the group. It is therefore possible that at this time pair bonds evolved for the protection of the mothers and their offspring, probably in response to the need to nurture the offspring for many years to ensure their survival to reproductive maturity. Monogamy, then, may have arisen as a strategy by which the woman obtains the permanent attentions of a man who will help her fend for their offspring, and the man is rewarded by having his sexual drive gratified by a woman who is sexually receptive throughout her reproductive cycle. Also, and most importantly, monogamy helps to ensure that the genes of each partner are passed on to the next generation. Sexual pleasure has therefore become very important in our species. If women could only enjoy sexual satisfaction at the time of ovulation (2–3 days every 28 days) this might jeopardise their ability to form lasting pair bonds. This is an example of structural and functional adaptations forming the basis of the social development and change which ultimately becomes an evolutionary selection pressure.

It is not known exactly when the family became a feature of human society, but it seems reasonable to speculate that it is a survival strategy based on reproductive pressures. From very early times, societies have imposed rules which govern the biological and social consequences of human sex drive to produce stability in communities. The sexual drive in humans is thus one of the primary factors which have contributed to the development of civilisation, and the structure of today's society is founded upon it. In many cases, particularly in the Western World, this has resulted in monogamy being the norm.

However, for our species, copulation has a greater significance than just reproduction. Inevitably, human sex drive also has less favourable influences on behaviour: it can be used in assault, for wielding power in relationships and for material gain. This is so because of the complexity of human behaviour, which is made possible by the relative size of the human cerebral cortex. A large brain is probably the single most distinguishing human feature. The evolution of the brain has enabled the development of an infinite variety of human behaviour, and a great deal of this behaviour influences and is influenced by sexuality.

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1.2 Ethnic and religious factors

As early people progressed from their lives as hunter–gatherers towards the first attempts at agriculture, the drive to produce their own offspring was translated to the struggle to ensure the fruitfulness of their livestock and crops. Promotion of fertility was central to the religious beliefs of these people, and fragments of these beliefs survive in the folk memory to the present day: Easter eggs, May Day ceremonies and spring weddings, to name but a few. At the heart of most modern religious systems is the belief that the fundamental difference between humans and other animals is that we have free will. One manifestation of this, as far as reproduction is concerned, is that we have broken away from biological necessity – each culture and subculture has developed its own patterns of behaviour.

The subject of ethnic and religious views on sexuality is vast and fascinating, but well beyond the scope of this book. Chapter 9 deals with some of the moral and ethical aspects of this which are deeply rooted in our various belief systems. Study and discussion of the many ethnic approaches and religious beliefs about sexuality and reproduction may help us to come to a clearer and more tolerant understanding of one another in our increasingly pluralist society.

1.3 Human reproduction – an overview

Issues surrounding human reproduction have been central to the development of society, because they are of such fundamental importance to us all. The scientific revolution which has enabled us to manipulate reproduction to the extent that we can control fertility and, to some extent, infertility, has gathered enormous momentum in the past decade, and this has raised public awareness of these issues. However, perhaps because it is so central to our lives, the subject of human reproduction is extremely complex, and coming to an understanding of it requires consideration not only of sociology and psychology, but also of the underlying biochemistry, as well as the structure and function of the reproductive cells, tissues and organs.

While focusing on the biology of human fertility and infertility, this book will attempt to reflect the complexity of this topic by, where appropriate, setting the biological issues into a social context.

This is because our lives are, to a very great extent, controlled by others, and the pressure produced by the exponential increase in human population has been an important factor in the rise of the technology which has enabled us to control it.

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TWO

Gamete production

Omnis cellula e cellula, 'All cells from cells' stated the German clinician Rudolf Virchow in 1855. From the beginning of evolution, the cells constituting the bodies of all life on Earth have come from pre-existing cells. More than any other characteristic of life, the ability to reproduce distinguishes the living from the non-living, and the process of reproduction is based on the cell cycle, the turn of which is dependent on cell division.

2.1 Cell cycle

Along with all other living things, except bacteria and cyanobacteria, the bodies of human beings are made up of eukaryotic cells. The vast majority of these cells are continually renewed and replaced by a form of cell division. This complex but ordered process involves duplication of the genetic material (DNA) in the nucleus of the cell, followed by its division into two equal portions, the migration of the portions to opposite sides of the cell (this part of the process is called **mitosis**), and finally the division and partition of the cytoplasm and its contents (**cytokinesis**).

A full cell cycle is that period from the end of one mitosis to the beginning of the next (figure 2.1). Division is the shortest phase of the cell cycle, and represents 5–10% of the total cell cycle time. Known as the M (or mitotic) phase, it is separated from the next M phase in the cycle by **interphase**, in which the cell is metabolically active and performs whatever functions for which it is adapted. After M phase is G1, or a gap phase, which occupies about 30–40% of the cycle during which the cell is metabolically active and is often increasing in size following division. In genetic terms it functions with the same amount of DNA as it received from the parent cell. During the S phase (30–50%) which follows G1, the cell synthesises new DNA. Another gap phase, G2, follows (10–20%) during which the cell prepares for the next mitosis, and another cycle, by replicating its organelles. So, for every cell that enters mitosis two emerge, each continuing through the subsequent cycle as independent entities.

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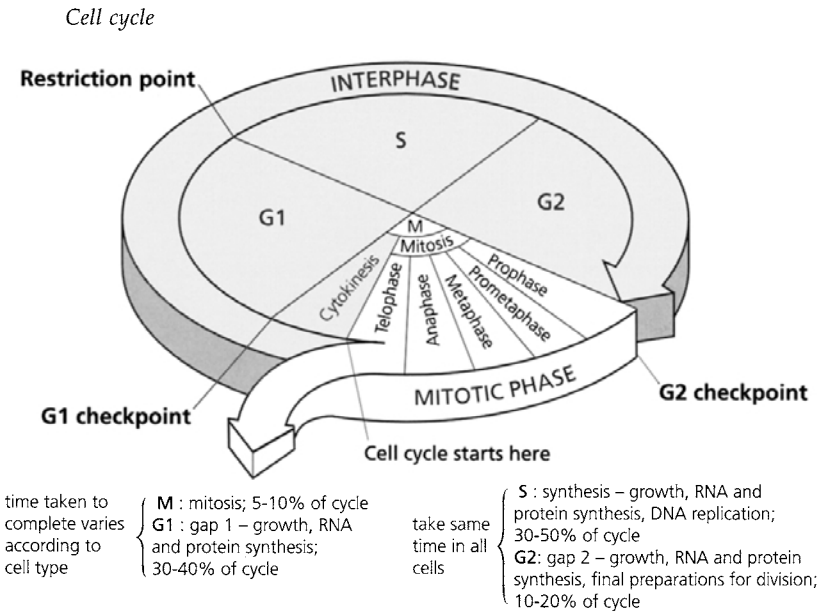

Figure 2.1 The cell cycle. The entire reproductive life of a eukaryotic cell is a 4-stage cycle. A full cycle is that period from the end of one mitosis to the beginning of the next. M is the mitotic phase during which the nucleus divides. This is followed by G1, the first gap phase, after which comes the S phase when the cell synthesises new DNA. A second gap phase, G2, follows, and at the end of this the cell enters M once more.

The length of a cell cycle varies considerably from one cell type to another, and from one species to another. In humans there are about 10^{13} cells, each different type cycling at a different rate, the shortest cycles being those which take place during early embryonic development. In the liver cell, however, the cell division cycle can take more than a year. Two notable exceptions to this are nerve and muscle cells, which do not divide but remain arrested in the G1 phase for their entire life.

Control of the cell cycle is an important focus of current research in cell biology, because of its relevance to our understanding of cancer. In all cells the stages S to M always take a fixed length of time; G1 is the phase which varies. At the end of G1 is a point of no return, known as the **restriction point**. It is thought that a protein accumulates (or not) during G1 which enables the cell to get past the restriction point and enter the S phase. Once the restriction point is passed, the cell cycle turns through S, G2, M and G1 again. Other such checkpoints on the cell cycle are thought to operate at the end of G2 and at metaphase.

Duplication of the DNA is made more reliable by the grouping and folding of the molecules into compact structures called **chromosomes**. The chromosomes are very long molecules, short sections of which encode for specific proteins. These sections are called **genes**, and the entire genetic complement of a cell is known as the **genome**. The fact that the process of

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DNA replication, and hence duplication of the entire genome, so rarely goes wrong, and faithful copies are made time after time, is the molecular basis of the amazing miracle of life.

All cells are genetically programmed to divide a certain number of times, and this number varies with cell type. One notable outcome of the Human Genome Mapping Project, a world-wide scientific collaboration to identify all human genes, is the discovery of the genetic mechanism for this 'programmed cell death'. It is not impossible that scientists may, in the not-too-distant future, be able to manipulate this gene such that cell death might be postponed, and life possibly prolonged. Inevitably, this will raise a huge moral debate.

2.2 The significance of meiosis

Multicellular organisms reproduce sexually. This process is the result of the fusion of two cells, as opposed to the fission of one cell to make two as in the case of unicellular asexual reproduction. The significance of this is that the resulting individual possesses a new and unique genome which is quite distinct from that of either parent. It is in the obvious and subtle differences between parent and offspring that the potential for change through variation lies. The process by which these differences are produced involves a type of cell division which occurs during the production of the gametes (sperm and oocytes, or eggs) and which results in a halving of the genome. Every eukaryotic organism has a characteristic **diploid** chromosome number – in humans it is 46. This means that in every **somatic** cell (all body cells except the gametes) there are 46 chromosomes. The type of cell division which produces the gametes is known as **meiosis**, and it results in each human sperm and oocyte containing 23 chromosomes – the **haploid** number. During the process of fertilisation the diploid number of chromosomes is restored, and every subsequent turn of the cell cycle during embryological development, growth to maturity and body maintenance results in two diploid daughter cells. However, very early in embryonic life (chapter 4) a germ cell line is determined, and two distinct cell populations result: that is somatic cells and germ cells. The germ cells ultimately give rise to the gametes. These two cell lines remain distinct throughout life, and the processes of mitosis and cytokinesis retain the full genome in all the cells of the body except the germ cells.

A full account of the process of meiosis can be read in *Heredity and human diversity* by Stephen Tomkins (CUP, 1989), but the essential point about it is that it consists of two cell cycles, only the first of which involves duplication of the DNA. The prophase of the first meiotic division is specialised to allow exchange of sections of genetic material between the chromosomes. This process is called crossing-over, and results in a

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recombination of genes which greatly increases the variability of the gametes. After the extended and complex prophase, the chromosomes line up on the equator of the cell in homologous pairs so that the individual members of each pair are pulled to opposite poles. Separation and migration of the chromosomes is followed by a short interphase which separates the two divisions, during which there is no DNA synthesis in the S phase. The second meiotic division is quicker and simpler than the first, and the events are very similar to those in mitosis: the chromosomes line up on the equator of the cell, the centromere of each chromosome divides and the sister chromatids separate.

2.3 Hormonal control of gamete production

The human reproductive system, in common with that of all other mammals, is under the control of the central nervous system (CNS). The gonads (ovaries and testes) have two main functions: to produce gametes and to produce hormones. The male sex hormones are called **androgens**, the most important of which is **testosterone**, and the female hormones are the **oestrogens** and **progesterone**. Production of the sex hormones by the testis and ovary is under the control of gonadotrophic hormones secreted by the anterior lobe of the pituitary gland just beneath the brain (figure 2.2). The gonadotrophic hormones are f**ollicle stimulating hormone** (FSH) and **luteinising hormone** (LH). In common with all endocrine secretions, they are released directly into the bloodstream in which they travel until they reach their target organs. These organs are recognised by specific receptor proteins in the cell surface membranes of the target organ cells.

The pituitary gland is itself under the control of a particular part of the floor of the brain, called the **hypothalamus**, to which it is physically connected by a specialised stalk containing portal blood vessels. These vessels provide a route for transfer of information from the hypothalamus to the pituitary gland. The hypothalamus contains neurones which, unlike other neurones, secrete hormones instead of **neurotransmitters** that help in the transmission of nerve impulses. These hormone-secreting neurones are called **neuroendocrine** cells, but in many other respects they function similarly to ordinary neurones: they have cell bodies, axons, dendrites and so on, and they receive neural stimulation from other neurones via synapses. The hormones secreted by the hypothalamus, sometimes called **releasing factors**, enter the portal system in the pituitary stalk and, on reaching the anterior lobe of the gland, stimulate it to release its hormones. The hypothalamic releasing factor responsible for secretion of the gonadotrophic hormones FSH and LH is called **gonadotrophin releasing hormone (GnRH).**

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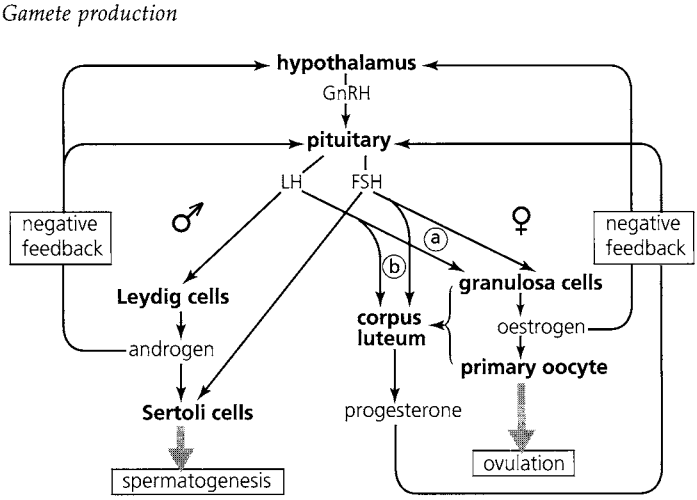

Figure 2.2 Hormone interactions between the hypothalamus, pituitary and gonads (*a*) follicular phase of the ovarian cycle; (*b*) luteal phase of the ovarian cycle.

The significant point about the involvement of the hypothalamus is that it is here that neural stimuli are changed into chemical stimuli. In some animals this is extremely important, as successful reproduction is often linked to a number of external factors, such as the seasons, proximity of others of the species, and so on. The animal is made aware of these factors by a variety of visual, tactile and olfactory cues, which are fed into the CNS and eventually reach the hypothalamus where they are processed, amplified and changed into chemical information in the form of GnRH. The information is further amplified and passed on by the pituitary to the gonads in the form of FSH and LH. The gonads respond by producing sex hormones which act on a variety of target organs, including the pituitary itself.

Although the extent to which external factors affect human fertility is not fully understood, this integrated CNS–endocrine information system coordinates all aspects of reproduction, including sexual function and maintenance of secondary sexual characteristics.

2.4 Gametogenesis

The cells which give rise to the gametes (eggs and sperm) are known as **primordial germ cells** which arise in the embryo during the fourth week after fertilisation. During the fourth to sixth week of embryonic development these, as yet unspecialised, cells migrate to a position within the embryo where they will ultimately bring about the formation of the gonads. During this migration they multiply continuously by mitosis. A

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