

Appendix

A Gross Anatomical Study of the Peripheral Nerves Associated with Reproductive Function in the Female Albino Rat

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I. INTRODUCTION

Although there are a number of excellent anatomical studies of central neuro-endocrine mechanisms, there is no single comprehensive dissection guide to the peripheral neural apparatus. The purpose of this appendix is to provide a clear description of the peripheral neuroanatomy associated with reproductive function in the female rat.

This guide deals with six major peripheral nerves: femoral, genitofemoral, pelvic, hypogastric, pudendal, and caudal cutaneous femoral. The anatomy of these nerves has been described in various species, including the albino rat, following Langley and Anderson's classic paper of 1896 (see Bradley and Teague, 1972; Carlson and DeFeo, 1965; Greene, 1968; Hebel and Stromberg, 1976; Kollar, 1952; Langworthy, 1965; Purinton *et al.*, 1973). However, gaps in these anatomical descriptions still exist. For example, some studies are primarily devoted to electrophysiology, and the accompanying anatomical descriptions were limited to the service of specific physiological experiments. Furthermore, the anatomical studies cited often are large and do not provide great detail on the peripheral genital apparatus per se. Finally, there is no single

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source that pulls all of the information together in one place with accompanying diagrams for use by investigators in reproductive anatomy and physiology.

In order to facilitate understanding of the various nerves, muscles, organs, etc. discussed below, we have used the nomenclature with which most readers are familiar, that used by Greene (1968). In order to insure accuracy, we have followed Greene's terminology with the nomenclature used in *Nomina Anatomica Veterinaria* (World Association of Veterinary Anatomists, 1973), placed in parentheses, as well as using the NAV nomenclature in all figures. Figure 1 gives the major anatomical landmarks used for orientation and provides a useful reference throughout. Although anterior and posterior are used to facilitate comparison with the standard work by Greene, the accepted terminology for quadrupeds is cranial and caudal (World Association of Veterinary Anatomists, 1973). Anterior and posterior are now reserved for upright, bipedal animals.

II. METHODS

One hundred female rats were dissected in order to ascertain the anatomical relationships of the nerves innervating urogenital structures as well as other areas associated with reproductive function. The animals were sacrificed by overdose of anesthetic. All dissections were performed on fresh specimens in order to enhance the contrast between nervous and connective tissue. Nerves were followed from their origin at the spinal cord to the organs and muscles that they innervated with the aid of a Zeiss stereoscopic dissecting microscope. All animals were approached from the ventral aspect, and the descriptions are based upon that approach.

III. RESULTS

A. Femoral Nerve

The femoral nerve (N. femoralis) is formed by contributions from the third and fourth lumbar nerves (Greene, 1968). It travels caudolaterally, dorsal to the psoas muscle group and ventral to the body of M. iliacus. The nerve has been divided into two divisions: anterior (Ramus musculares) and posterior (N. saphenus).

The anterior division consists of those nerve branches given off to M. psoas major and M. iliacus, as the femoral nerve passes between the fascial planes separating the two (Fig. 2). It then continues on to innervate M. pectineus, passing dorsal to the external iliac vein (Vena iliaca externus), and enters the muscle on its dorsal side prior to the final branching as shown in Fig. 2.

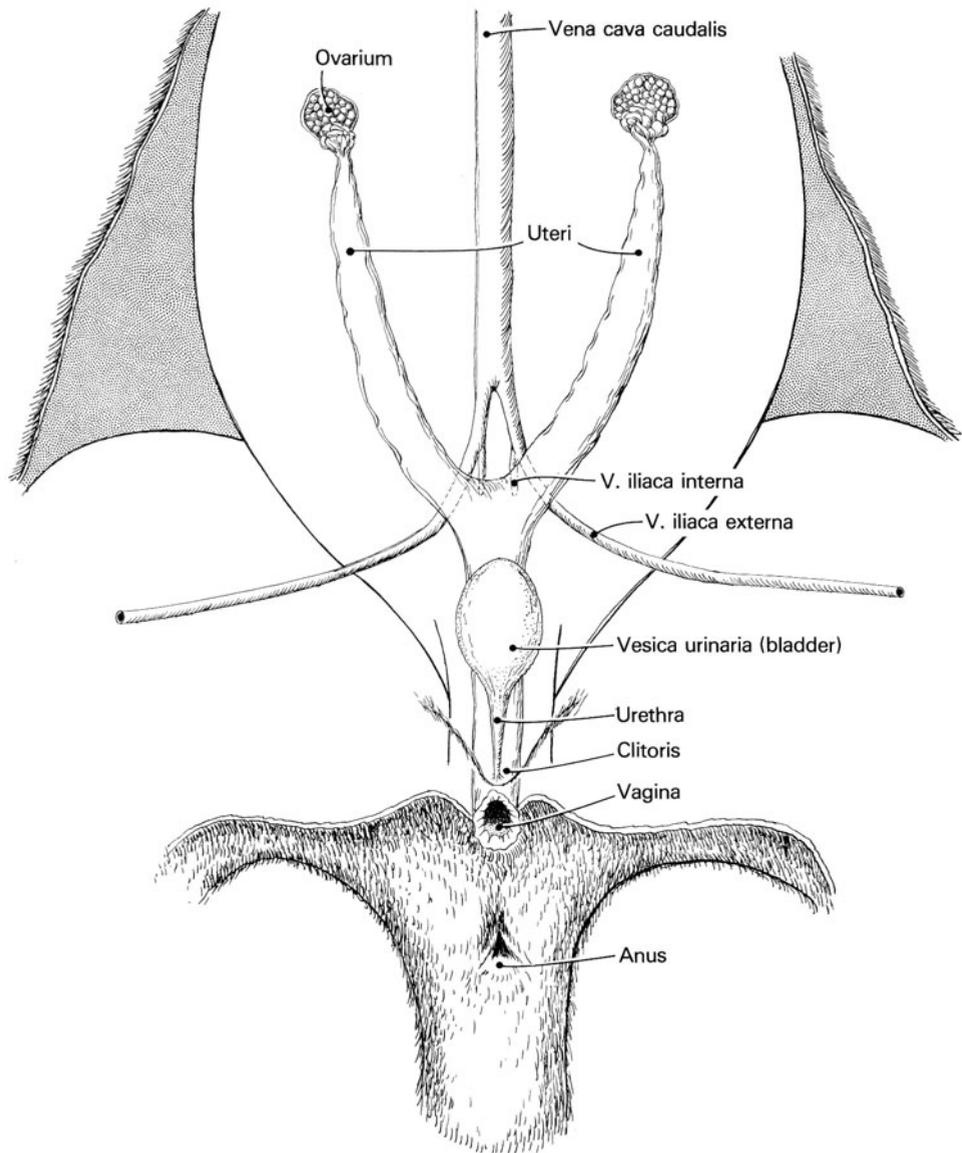


Figure 1. General anatomical landmarks, ventral view. In this and all subsequent figures, nomenclature used will be that found in *Nomina Anatomica Veterinaria* (World Association of Veterinary Anatomists, 1973). Abbreviations: A, Arteria; L, Ligamentum; M, Musculus; MM, Musculi; N, Nervus; V, Vena.

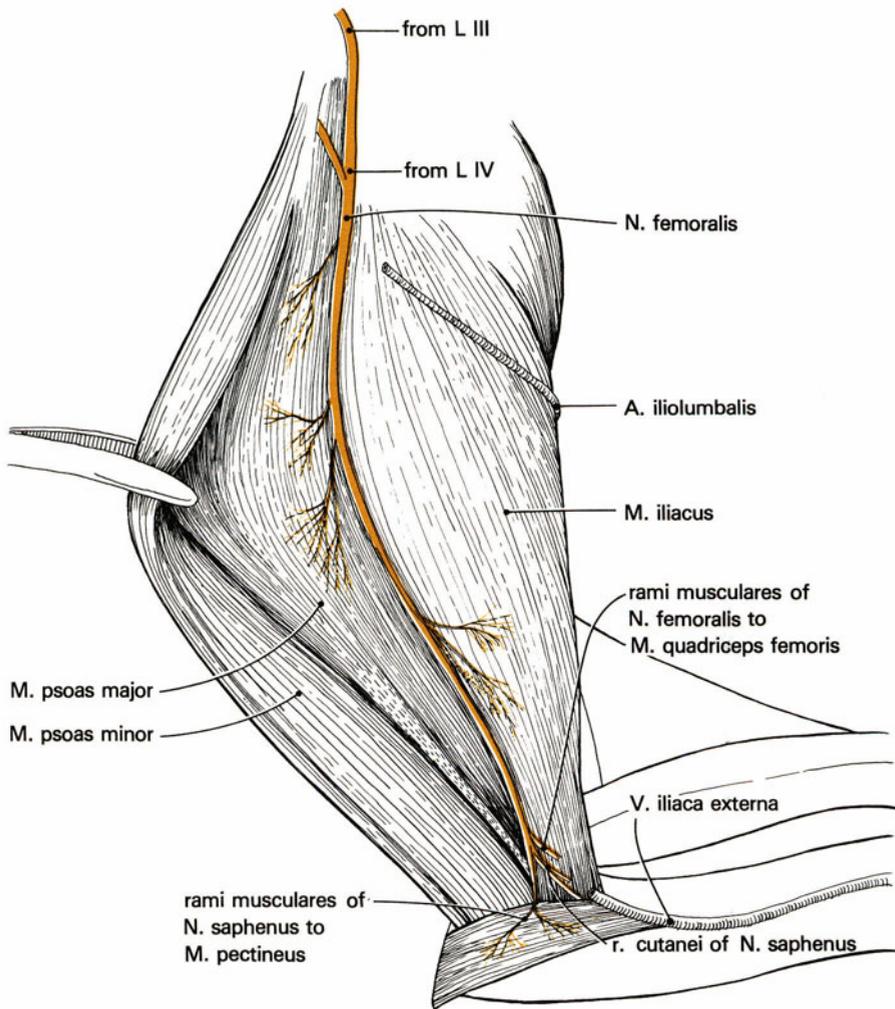


Figure 2. Nervus femoralis, ventral view, with MM. psoas reflected medially.

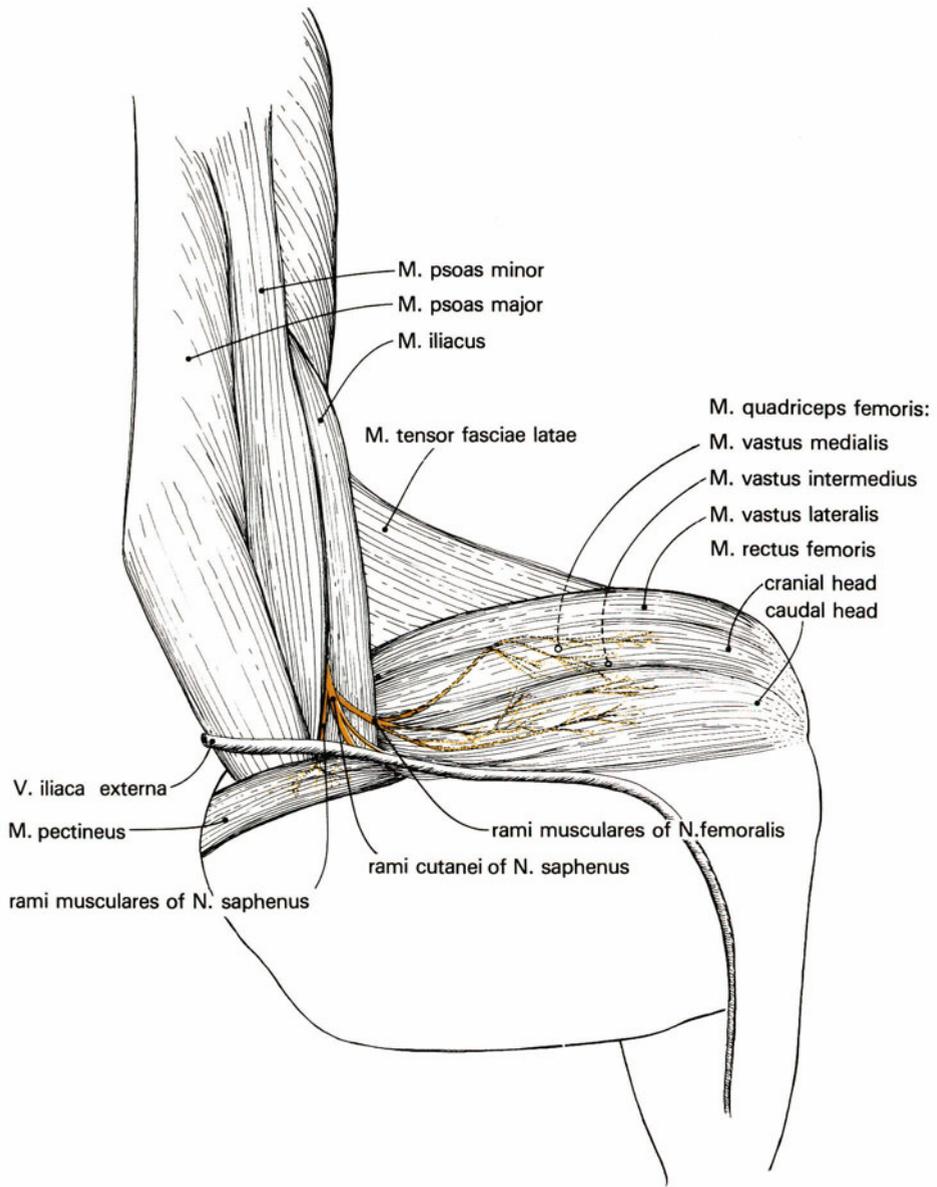


Figure 3. Nervus femoralis, ventral view, with innervation of M. pectineus and MM. quadriceps detailed.

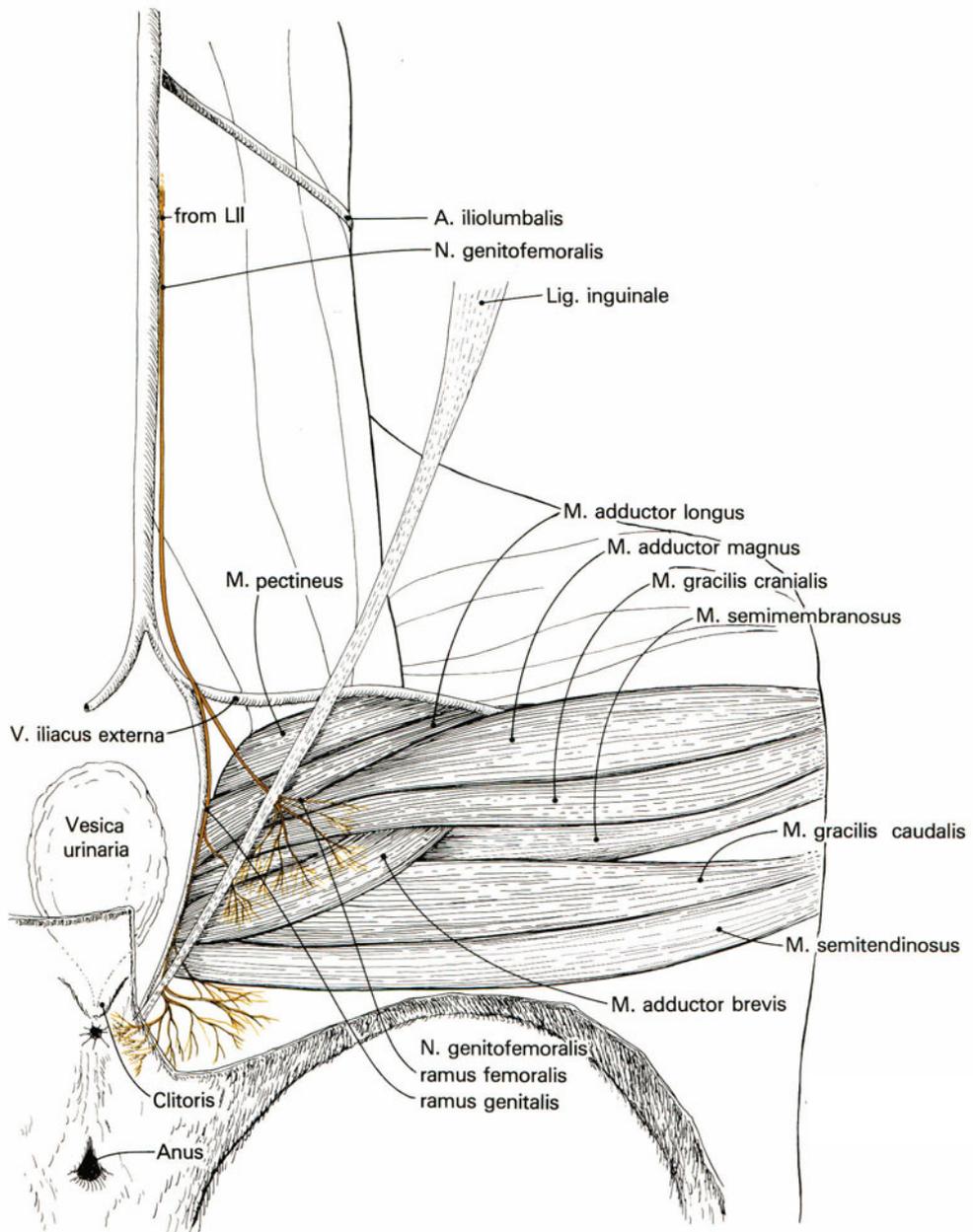


Figure 4. Nervus genitofemoralis, ventral view.

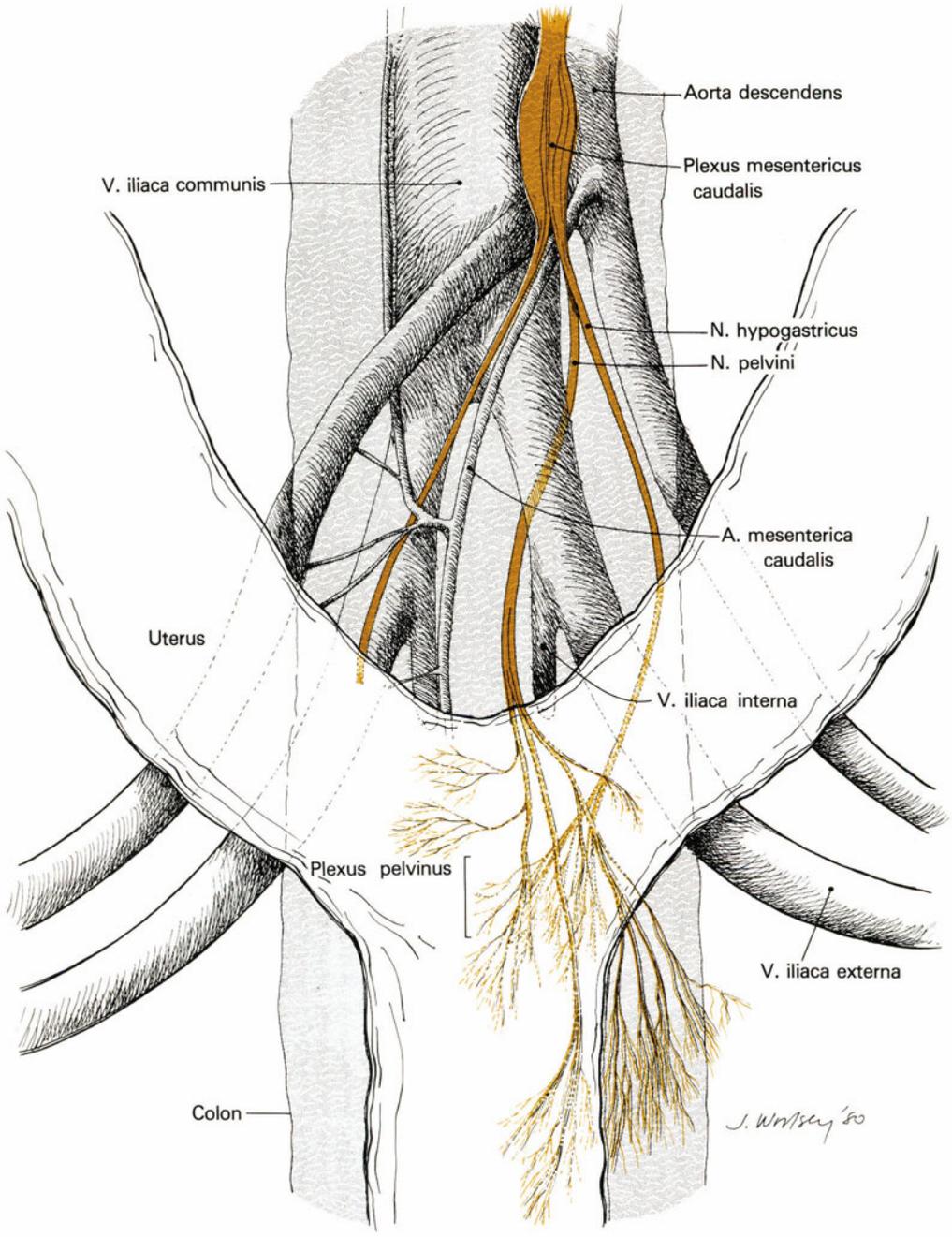


Figure 5. Plexus pelvinus, ventral view, with course of NN. pelvini and hypogastricus shown.

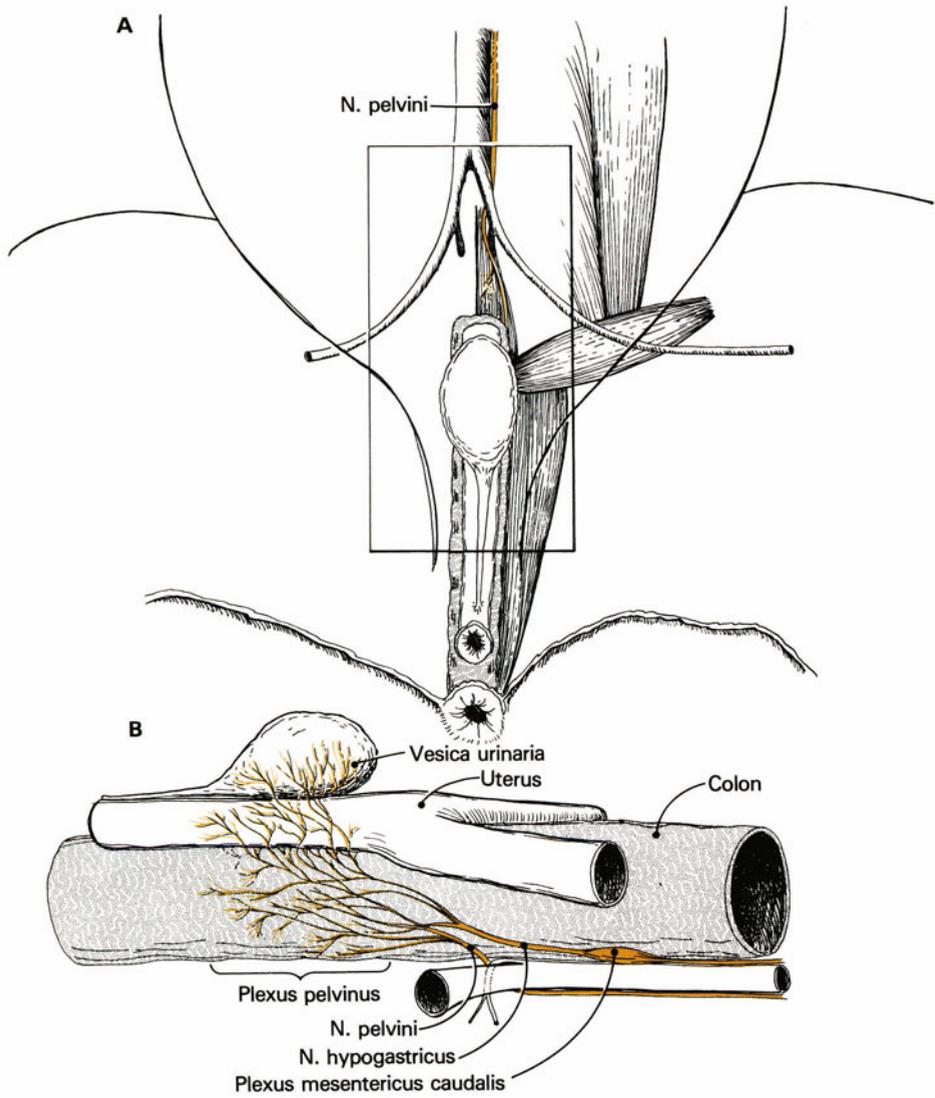


Figure 6. A, Nervus pelvini, ventral view, detail of course alongside Vena cava caudalis. B, Plexus pelvini, lateral view.

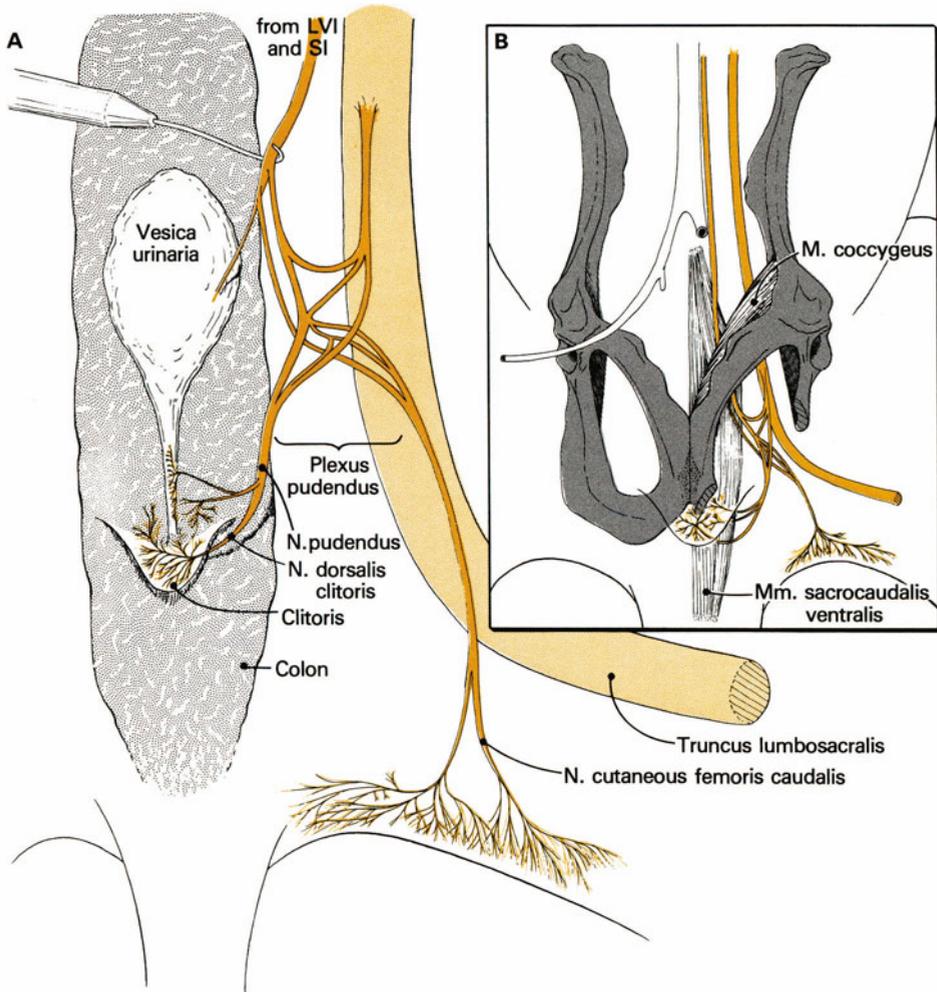


Figure 7. A, Nervus pudendus, ventral view, with detail of innervation of caudal skin (N. cutaneus femoris caudalis) and the urethra and clitoris (N. dorsalis clitoris). B, Nervus pudendus with relationship to M. coccygeus; MM. sacrocaudalis ventralis are detailed.

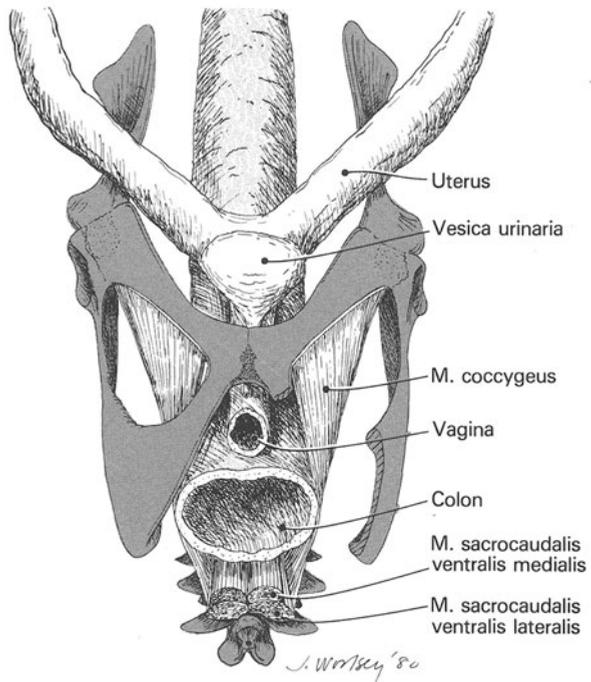


Figure 8. Musculus coccygeus and MM. sacrocaudalis ventralis, oblique caudocranial view.

The posterior division also splits into two divisions: a muscular branch (*Ramus musculares* and the saphenous nerve (*Ram cutanei*). The saphenous nerve is well-known and needs no further description here (we refer the reader to Greene, 1968). The muscular branch innervates *M. quadriceps femoris* (Fig. 3). *M. quadriceps femoris* is the well-known muscle group situated in the upper thigh and is composed of four muscles: *M. vastus lateralis*, *M. vastus intermedius*, *M. vastus medialis*, and *M. rectus femoris*. The distribution of the innervation to these muscles is detailed in Fig. 3.

B. Genitofemoral Nerve

The genitofemoral nerve (*N. genitofemoralis*) emerges at the level of L2 and travels caudally along the border between the psoas muscle group and the aorta. Just caudal to the aortal bifurcation (Fig. 4), it divides into two branches that pass ventral to the common iliac vein (*Vena ilaca communis*): the external spermatic (*Ramus genitalis*) and the lumboinguinal branch (*Ramus femoralis*). The latter branch innervates the skin of the cranial femoral triangle, the area overlying the muscles innervated by the posterior division of the femoral nerve (see Fig. 3). The external spermatic branch travels farther caudally, giving off branches to the skin of the caudal femoral triangle, through the inguinal canal, and finally innervates the skin immediately adjacent to the genitalia as well as the *Labium majus* (*Labium pudendi*) (Greene, 1968).

C. Pelvic and Hypogastric Nerves

These two nerves must be described together in order to understand their anatomical relationship. The two nerves intermingle in the pelvic plexus (*Plexus pelvinus*) (Figs. 5, 6B) located on the lateral wall of the rectum, dorsal to the uterine junction. The hypogastric nerve (*N. hypogastricus*) emerges as a bilaterally paired nerve from the inferior mesenteric plexus (*Plexus mesentericus caudalis*) (Fig. 5), a ganglion located on the ventral surface of the inferior mesenteric artery (*A. mesenterica caudalis*) at the bifurcation of the aorta (Marshall, 1970).

The inferior mesenteric plexus is one of a network of sympathetic plexus and ganglia that more or less cover the ventral surface of the aorta and *Vena cava* (Kuntz, 1965). They receive input from the sympathetic chain ganglia via the lumbar splanchnic nerves (*Nn. splanchnici lumbales*). From the inferior mesenteric plexus, the nerve travels laterally and caudally, usually within a mass of fatty tissue, more or less defining the side of an ellipse formed by the iliacal vessels and the uteri. It descends dorsally from the level of the dorsal extent of the uterus to the lateral surface of the colon as it explodes into the pelvic plexus.

The pelvic nerve (*N. pelvini*) provides the parasympathetic component of

the plexus (Bradley *et al.*, 1974; Carlson and DeFeo, 1965; Langworthy, 1965). The nerve emerges from S1 and S2 and travels caudally and slightly laterally. It runs immediately ventral to the pudendal nerve (N. pudendus) and traverses medial to the internal iliac vein (Vena iliaca interna) as the latter descends dorsally. From there, it arches medially, coming to rest on the lateral surface of the colon. (Fig. 6A).

The pelvic plexus is a delicate structure in the female rat. From the plexus, fine strands innervate the rectum, vagina, clitoris, urethra, urinary bladder, and cervix (Langworthy, 1965). Much work has been devoted to the details of visceral innervation via the pelvic plexus both extrinsically and intrinsically (Bradley and Teague, 1972; Langley and Anderson, 1896; Marshall, 1970; Purinton *et al.*, 1973). For details, we refer the reader to these papers.

D. Pudendal and Caudal Cutaneous Femoral Nerves

Fibers arising from L6 and S1 that ultimately contribute to the pudendal plexus form a trunk that travels caudally just deep to the pelvic nerve. In fact, between the vertebrae and the internal iliacal vessels, they run duplicate courses, the only difference being that the trunk lies dorsal (i.e., "deep" in our figures) to the pelvic nerve along the way. As the pelvic nerve rises caudal to the internal iliac (Fig. 6A), the trunk dives dorsally under the ascending ramus of the pubis (Ramus cranialis os pubis), traveling between the coccygeus muscle (M. coccygeus) and the caudal flexors (Mm. sacrocaudalis ventralis) (Fig. 7B). As the trunk continues caudally, deep to the obturator foramen (Foramen obturatorum), it meets collaterals from the lumbosacral trunk (Truncus lumbosacralis) in the so-called pudendal plexus (Plexus pudendus) (Fig. 7A). The Ramus musculi coccygei, a series of delicate fibers innervating the coccygeus muscle, is given off just prior to the plexus.

The plexus itself is a fine structure that can easily be separated into its component parts. A narrow branch of the lumbosacral trunk interacts with the pudendal trunk to produce the plexus which lies deep to the caudolateral aspect of the obturator foramen. From there, two nerve groups emerge. Laterally, the caudal cutaneous femoral nerve (N. cutaneous femoris caudalis) travels to the caudal extent of the animal, innervating the skin that lies in the trough formed between the tail and thigh itself (Greene, 1968; Langley and Anderson, 1896). The medial nerve group is that of the pudendal nerve itself (N. pudendus), innervating the urethra and colon with fine branches while sending a prominent branch, the dorsal nerve of the clitoris (N. dorsalis clitoris), beneath the symphysis pubis to innervate the clitoris.

A brief mention of the relationship of the muscles of the pelvic diaphragm and the caudal flexors to the appropriate nerves will aid the reader in orienting himself and understanding the overall topography. The caudal flexors, brevis (M. sacrocaudalis ventralis lateralis) and longus (M. sacrocaudalis ventralis medialis), are shown in Fig. 8. They take their origins from the lumbar verte-

brae as far cranially as L5 and insert upon and throughout the tail (Greene, 1968). The coccygeus muscle is also illustrated in Fig. 8. It arises from the ventrocaudal ilium and inserts upon the tail with the caudal flexors (Green, 1968). The muscle known as Levator ani in many texts is absent in the female rat after day 18 of neonatal life (Hebel and Stromberg, 1976). The pudendal nerve travels medial to the coccygeus, within the pelvic diaphragm, to reach its ultimate destination. It is therefore necessary to remove much of the ventral aspect of the pelvis in order to properly visualize its intrapelvic course.

REFERENCES

- Bradley, W. E., and Teague, C. T., 1972, Electrophysiology of pelvic and pudendal nerves in the cat, *Exp. Neurol.* **35**:378.
- Bradley, W. E., Timm, G. W., and Scott, F. B., 1974, Innervation of the detrusor muscle and urethra, *Urol. Clin. North Am.* **1**(1):3.
- Carlson, R. R., and DeFeo, V. J., 1965, Role of the pelvic nerve vs. the abdominal sympathetic nerves in the reproductive function of the female rat, *Endocrinology* **77**:1014.
- Greene, E. C., 1968, Anatomy of the rat, *Trans. Am. Philosoph. Soc.* **XXVII**:1.
- Hebel, R., and Stromberg, M. W., 1976, *Anatomy of the Laboratory Rat*, Williams & Wilkins, Baltimore.
- Kollar, E. J., 1952, Reproduction in the female rat after pelvic nerve neuroectomy, *Anat. Rec.* **115**:641.
- Kuntz, A., 1965, *Autonomic Nervous System*, Third Edition, Lea & Febiger, Philadelphia.
- Langley, J. N., and Anderson, H. K., 1896, The innervation of the pelvic and adjoining viscera. Part VII: Anatomical observations, *J. Physiol. (Lond.)* **20**:372.
- Langworthy, O. R., 1965, Innervation of the pelvic organs of the rat, *Invest. Urol.* **2**:491.
- Marshall, J. M., 1970, Adrenergic innervation of the female reproductive tract: Anatomy, physiology and pharmacology, *Ergeb. Physiol.* **62**:6.
- Purinton, P. T., Fletcher, T. F., and Bradley, W. E., 1973, Gross and light microscopic features of the pelvic plexus in the rat, *Anat. Rec.* **175**:697.
- World Association of Veterinary Anatomists, 1973, *Nomina Anatomica Veterinaria*, Second Edition, International Committee on Veterinary Nomenclature, Vienna.

Index

- Acetylcholine, *see* Neurotransmitters
- ACTH, *see* Adrenocorticotropin hormone
- Adenohypophysis, *see* Anterior pituitary
- Adrenal hormones, 7, 107–108, 112, 291, 310, 313, 453–454, 497, 540
- Adrenocorticotropin hormone (ACTH)
- effects on learned behavior, 7
 - site of action on steroids, 50
 - species variation in, 7
 - structure of, 7
- Amygdala, 365
- Androgens (*see also* Adrenal hormones, Sexual differentiation, Steroid hormones)
- effects on hypothalamus, 539–540
 - effects on neurotransmitters, 473–474, 503–505
 - effects on pituitary, 230
 - and neural development, 506–510
 - receptors for, in brain, 473, 499, 527–529
 - synthesis of, 52
- Angiotensin II, and water balance, 8
- Anterior pituitary (*see also* Adrenocorticotropin hormone, Follicle-stimulating hormone, Growth hormone, Luteinizing hormone, Prolactin, Thyroid-stimulating hormone)
- anatomy of, 14–15, 356–358
 - effects on gonads, 50, 263–265, 302, 309–310
- Antidiuretic hormone (ADH), *see* Vasopressin
- Arcuate nucleus, *see* Hypothalamic areas
- Aromatization, 40, 499, 506–507
- Brattleboro rat, 14
- Circadian rhythms (*see also* Photoperiodism)
- entrainment of, 378, 396–400
- Circadian rhythms (*cont'd*)
- and estrous cycle, 310
 - and ovulation, 305–308
 - phase–response curve for, 398–400, 409–410
 - in photoperiodism, 395–396, 400–416
 - of photosensitivity, 351, 411–414
 - and pineal gland, 11, 391–392
- Copulation, *see* Sexual behavior
- Critical period, *see* Ovulation, Sexual differentiation
- Dopamine, *see* Neurotransmitters
- Estradiol, *see* Estrogens, Steroid hormones
- Estrogens (*see also* Adrenal hormones, Steroid hormones)
- effects on enzymes, 502–503
 - effects on hypothalamus, 534–539
 - effects on neurotransmitters, 473–474, 503–505
 - effects on pituitary, 230, 248, 250–260, 302–303, 502
 - effects on uterus, 288–289
 - and neural development, 506–510
 - receptors for
 - in brain, 254–255, 362, 473, 500, 527–529
 - in ovaries, 267
 - in pituitary, 260 - synthesis of, 52–53
- Estrous cycles (*see also* Menstrual cycles, Ovulation)
- behavioral estrous, 281–283
 - correlations among indexes of, 281, 287
 - in the dog, 321–322
 - four- and five-day cycles compared, 287–288, 291–293, 296–297

Estrous cycles (*cont'd*)

- in the guinea pig, 310–313
- in the hamster, 308–310
- hormonal profile of, 299–305
- and hypothalamic activity, 534–535
- lability of cycle length, 305
- mathematical model of, 305–308
- and olfactory stimuli, 355, 364–365
- and ovarian hormones
 - estrogens, 290–291
 - progestins, 292–293
- and ovarian morphology
 - corpora lutea, 286–287
 - follicles, 283–286
 - interstitial cells, 287–288
- and peptide hormones, 250–265
- and pituitary cytology, 294
- and pituitary hormones, 296–298
- in sheep
 - and estrous behavior, 314
 - and ovarian function, 314–315, 316, 319–320
 - and pituitary hormones, 315–316, 318, 321
- species differences, 312–313, 316, 318
- and uterine weight, 281
- and vaginal cytology, 280–281

Follicle-stimulating hormone (FSH) :

- receptors for, in follicles, 263
- release of, 254
- structure of, 8–9
- surges of, in ovulation, 304, 309–310, 315
- synergism with LH, 304

FSH *see* Follicle-stimulating hormone

GH, *see* Growth hormone

GHIF, *see* Hypothalamic hormones

Gonadal hormones, *see* Androgens, Estrogens, Progestins, Steroid hormones

Gonadotropins, *see* Follicle-stimulating hormone, Luteinizing hormone

Growth hormone (GH), structure of, 8

Growth hormone inhibiting hormone (GHIF), *see* Hypothalamic hormones

Hibernation, 388–391

Hippocampus, 366–367

Human chorionic gonadotropin, 9

Hypophyseal portal system, 6, 247, 357, 430–431

Hypophysiotropic area, *see* Hypothalamic areas

Hypophysis, *see* Anterior pituitary, Pars intermedia, Posterior pituitary

Hypothalamic areas

- arcuate nucleus, 113–115, 230, 255
- hypophysiotropic area, 247, 360
- medial basal area, 254–256, 360
- medial preoptic area, 252, 361–363, 538–539, 540
- medial preoptic nucleus, 362
- median eminence, 428
- paraventricular nucleus, 4, 13–14, 356–357
- preoptic area, 230, 252–253, 254
- suprachiasmatic area, 251–254, 428–430, 438
- suprachiasmatic nucleus, 230–231, 310, 351, 362, 386, 419
- supraoptic nucleus, 4, 13–14, 356–357
- ventromedial nucleus, 538–539

“Hypothalamic gonadostat,” role in puberty induction, 232–234

Hypothalamic hormones

- behavioral effects of, 495–496
- cellular mechanisms of, 435–436, 486–487, 494
- characterization of, 432–435
- control of by neurotransmitters, 443–445
- corticotropin releasing factor (CRF), 432, 438
- effects on pituitary hormones, 261–263, 436, 446–447
- during estrous cycles, 298–299
- follicle-stimulating hormone-releasing hormone (FSH-RH), 434
- growth-hormone inhibiting factor (GIF) (somatostatin), 6, 434, 438
- localization of, in brain, 437–439, 446, 494
- luteinizing hormone-releasing hormone (LHRH), 6, 116, 360, 362–363, 434–435, 438, 495
- mediation by ventricles, 360, 438, 495–496
- melanocyte stimulating hormone releasing factors (MSH-RF), 434
- as neurotransmitters, 447
- and puberty induction, 234
- receptors for, 435–436, 488–489
- as releasing factors, 6, 247, 249
- thyrotropin-releasing factor (TRF), 6, 432, 438

Hypothalamic–pituitary gonadal axis (*see also*

- Estrogens, Estrous cycles,
- Follicle-stimulating hormone,
- Hypothalamic hormones, Luteinizing hormone, Ovulation, Progestins)

description of, 232

early studies on, 243–250

as “long-loop” system, 250

Moore–Price model of, 244–246

- Hypothalamic (*cont'd*)
 role in puberty induction, 231
 and "short-loop" system, 265–266
 and "ultra-short-loop" system, 266
- Hypothalamus (*see also* Hypothalamic areas,
 Hypothalamic hormones,
 Hypothalamic–pituitary–gonadal axis)
 and control of pituitary hormones, 246–247,
 252–253, 356–368, 429–430
 as "final common pathway," 359–363
 and gonadal function, 427–428
 and hormone production, 4
 modulation by extra-hypothalamic areas, 367
 and ovarian function, 359–361
 and persistent estrus, 360
- Intermediate lobe, *see* Pars intermedia
- LH, *see* Luteinizing hormone
- LHRH, *see* Hypothalamic hormones
- Lordosis, *see* Sexual behavior
- Luteinizing hormone (LH)
 receptors for, in ovary, 263
 release of, 315, 440
 site of action, on steroids, 50
 structure of, 8–9
 surges of, and ovulation, 302, 309–310
- Luteinizing hormone-releasing hormone
 (LHRH), *see* Hypothalamic hormones
- Medial basal hypothalamus, *see* Hypothalamic
 areas
- Medial preoptic area, *see* Hypothalamic areas
- Median eminence, *see* Hypothalamic areas
- Melanocyte-stimulating hormone (MSH), *see*
 Pars intermedia
- Melatonin, *see* Pineal melatonin
- Menstrual cycles, in rhesus, 322–325
- Mullerian ducts, *see* Sexual differentiation
- Neurohypophysis, *see* Posterior pituitary
- Neurotransmitters
 distribution in brain, 77–82
 effects of drugs on, 73–75
 effects of hormones on, 470–474
 effects on sexual behavior
 female, 454–460
 male, 462–467
 mechanism of action, 68–70
 and prolactin secretion, 11, 445
 and prostaglandins, 71
 receptors for, 71, 73–75
 storage of, 68
 structure of, 65–66
- Neurotransmitters (*cont'd*)
 synthesis of, 65–68
 turnover of, 70
 visualization of, 76–77
- Norepinephrine, *see* Neurotransmitters
- Ovaries, *see* Estrogens, Estrous cycles,
 Ovulation, Progestins
- Ovulation (*see also* Estrous cycles)
 blockade by anaesthetics, 295, 298–299, 305,
 350–351, 361
 blockade by continuous light, 251, 294, 310,
 350–352, 367
 and copulatory stimulation, 325, 352–353
 critical period for induction, 295, 305, 362
 hypothalamic control of, 203, 230, 358–359,
 361–362, 428
 and light-dark cycle, 294–295, 305–308, 313,
 350–351, 362
 reflexive
 blockade by anaesthetics, 352
 in the cat, 327–329
 in the rabbit, 325–327, 363–364
- Oxytocin
 release of, 354–355
 structure of, 5, 13–14
 synthesis of, 14
- Pancreatic hormones, 7–8
- Paraventricular nucleus, *see* Hypothalamic
 areas
- Pars intermedia, of pituitary, and
 melanocyte-stimulating hormone
 (MSH), 7, 16–17
- Peptide hormones, *see* Hypothalamic hormones
- Photoperiodism (*see also* Circadian rhythms,
 Seasonal breeding)
 and circadian rhythms, 391, 400–414
 and circannual rhythms, 378, 393
 ecological significance of, 380–381, 417–418
 mechanisms of, 393–396
 and photorefractoriness, 378–381
 and pineal melatonin, 382–386, 418–419
 and pituitary, 387–388
 and testicular function, 382, 388, 408
- PIF, *see* Hypothalamic hormones,
 Neurotransmitters
- Pineal melatonin, 11–12, 382–388, 391–392,
 418–419
- Portal system, *see* Hypophyseal portal system
- Posterior pituitary (*see also* Oxytocin,
 Vasopressin, Vasotoxin)
 anatomy of, 13
 and hypothalamus, 13–14, 356–357
 and neurophysins, 6, 14

- Pregnancy (*see also* Pseudopregnancy)
 and copulatory stimulation, 353
 and olfactory stimuli, 355–356
- Pregnant mare serum gonadotropin (PMSG), 9
- Preoptic area, *see* Hypothalamic areas
- Progesterone, *see* Progestins, Steroid hormones
- Progestins (*see also* Adrenal hormones, Steroid hormones)
 effects on hypothalamus, 540–541
 effects on neurotransmitters, 473–474, 503–505
 effects on pituitary, 232, 250–256, 260–261, 302–303, 502
 receptors for
 in brain, 254–255, 362, 498–499
 in ovaries, 267
 in pituitary, 260
 synthesis of, 52
- Prolactin
 and luteal function, 250, 311
 release of, 259–261, 353
 structure of, 8
 surges of, in ovulation, 304, 316
- Prolactin-inhibiting hormone (PIF), *see* Hypothalamic hormones, Neurotransmitters
- Pseudopregnancy (*see also* Pregnancy)
 and hormone production, 254, 264, 353
 induction of, 247–249, 353
 and luteal function, 247
- Puberty
 description of, 229–230
 and gonadal function, 229–234
 in humans, 236–238
 and neural function, 236–237
 neuroendocrine mechanisms of, 230–231
 and olfactory stimuli, 237, 355
 and pineal, 237
 and pituitary function, 233–234
- Releasing hormones, *see* Hypothalamic hormones
- Reticular formation, 367–368
- Seasonal breeding (*see also* Photoperiodism), 313–314, 321, 327, 350–351, 386
- Septum, 365
- Serotonin, *see* Neurotransmitters
- Sex determination, by chromosomes (*see also* Sexual differentiation), 91–94, 102–103, 167–168
- Sex reversal (*see also* Sexual differentiation, Sexual dimorphism), 162–164, 172, 177
- Sexual behavior
 bipotentiality of, 215–216
 in birds, 203–205
 female
 effects of drugs, 453–454
 effects of neurotransmitters, 454–460, 468–469
 and gonadal hormones, 127–129, 166, 289, 305
 and hypothalamus, 538–539
 and LHRH, 495
 measurement of, 452
 species differences, 452
 in fish, 177–178
 heterotypical, 140–141, 459–460, 467–468
 human, 468–469
 in insects, 170
 male
 effects of neurotransmitters, 462–467
 and gonadal hormones, 127–129
 and LHRH, 495
 measurement of, 461–462
 and medial preoptic area lesions, 540
- Sexual differentiation (*see also* Sex determination, Sex dimorphism, Sex reversal)
 in amphibia, 179–186
 and aromatization, 144–147
 in birds, 191–210
 and critical periods, in nonmammalian species, 170, 172–175, 180–181, 185
 disturbances of, 103–109
 effects of maternal hormones, 116–117, 168–169
 evolution of, 217–219
 in fish, 173–178
 and freemartinism, 89–90, 167
 of genitals, 98–102, 199–200
 of gonodal ducts, 91–97, 167, 100–202
 in invertebrates, 169–173
 of mammaries, 99–100
 of neural structure, 141–142, 509–510
 of neurochemical function, 142, 510
 of neuroendocrine function, 109–117, 142–143, 202–203, 208
 and nongonadal hormones, 167
 of nonsexual behaviors, 147–150
 overview of, 102–103, 112, 163–164, 216–217
 of reproductive structures, 173–174, 179–184, 186–202
 in reptiles, 186–191
 of sexual behavior, 129–144, 178, 184–185, 205–210

- Sexual differentiation (*cont'd*)
 species differences in, 93–94, 99, 111, 115–116, 171–173, 191, 204–205, 211–217
- Sexual dimorphism (*see also* Sex reversal, Sexual behavior, Sexual differentiation)
 in amphibia, 179–180
 in birds, 191, 192, 204, 205, 210
 in fish, 173
 in reptiles, 186
 substrate of, 164, 166
- Somatostatin, *see* Hypothalamic hormones
- Somatotropin, *see* Growth hormone
- Steroid hormones (*see also* Adrenal hormones, Androgens, Estrogens, Progestins)
 chemistry of
 definition of steroid, 22
 measurement of, 53, 58–61
 models of structure, 22–23
 nomenclature of, 27–29
 synthesis of
 and aromatization, 40
 enzymes, 38–44
 parental molecules, 23–27
 and pituitary hormones, 263–264
 precursors, 44–50, 52–53
 effects on enzyme activities, 503
 effects on hypothalamus, 534–541
 effects on neurotransmitters, 473–474, 503–505
 effects on pituitary hormones, 230, 248, 250–251, 256–257, 260, 302–303
 effects on pituitary sensitivity, 256–260, 502
 effects on uterus and vagina, 288–289
 genomic action of, 487–488, 506–510
 localization in brain, 520–529
 and neural development, 506–511
 and olfactory stimuli, 355–356
 radiographic localization in brain, 520–529
- Steroid hormones (*cont'd*)
 receptors for
 in brain, 255, 362, 473, 498–503, 520–529
 in ovaries, 267
 in pituitary, 260
 and sexual behavior, 127–129, 166, 289, 305
- Suprachiasmatic nucleus, *see* Hypothalamic areas
- Supraoptic nucleus, *see* Hypothalamic areas
- Testes, *see* Androgens, Photoperiodism, Sexual differentiation, Steroid hormones.
- Testosterone, *see* Androgens, Sexual differentiation, Steroid hormones
- Thyroid hormones, 10, 15, 492–493, 496, 505–506
- Thyroid-stimulating hormone (TSH)
 hypothalamic control of, 230, 257–261, 357–358, 427–430, 439–443
 steroid action on, 230, 248, 250–251, 256–261, 302–303
 structure of, 8
- Thyrotropin-releasing hormone (TRH), *see* Hypothalamic hormones
- TRH, *see* Hypothalamic hormones
- TSH, *see* Thyroid-stimulating hormone
- Vasopressin
 as antidiuretic hormone (ADH), 13
 behavioral effects of, 495
 as corticotropin-releasing factor, 431–432
 evolution of, 4–5
 structure of, 4–5, 14
 synthesis of, 14
- Vasotocin, 4–5, 13
- Wolfian ducts, *see* Sexual differentiation