Spinal Control of Sexual Reflexes: An Overview from Studies in Animal Models

Lesley Marson

Central nervous system control of female genital arousal and climax has been reviewed from data obtained in animal studies. Sensory inputs from the pelvic organs are mediated via the pudendal nerve (motor) and pelvic and hypogastric nerves (autonomic). The afferents of these nerves that relay sensory information terminate in L6-S1 and T13-L3. Interneurons located in the spinal gray (T13-S1), especially in the dorsal gray, commissure and surrounding the intermediolateral cell column are important in relaying afferent information to spinal efferent neurons. These interneurons also send messages to the brain. Vagal innervation of the pelvic organs may supplement the spinal systems and may be important in relaying sensory information after spinal cord injury. Key words: *interneurons, pelvic afferents, pelvic efferents, spinal pathways*

Very little is known about the central nervous system (CNS) pathways that control sexual reflexes in the human female. Much of what we presume to be true is based on animal studies and studies in males. Because a basic understanding of the components of female sexual function is lacking, it is difficult to relate dysfunction to a particular process or system. Studies that attribute changes in specific components of sexual function (desire, arousal, orgasm, pain, etc.) to spinal cord injury (SCI) may help differentiate the regulation of the female sexual response. Furthermore, these studies may provide important information on the basic anatomy, physiology, and psychology of female sexual function. A few studies have examined female sensory and pain responses after SCI in association with sexual function.[1–3] More studies are required to fully understand the organization of sexual responses and how they are affected by different SCIs.

This article will provide an overview of what is presently known about the spinal regulation of female genital responses. The majority of the information presented is from animal experiments on rodents. The autonomic innervation of the pelvic organs has been previously reviewed.[4–6] The pelvic (parasympathetic) and the hypogastric (sympathetic) nerves convey information from the internal pelvic organs, and the pudendal (somatic) nerve conveys most of the sensory stimuli from the external genitalia and perigenital areas. These nerves also control the contractile and blood flow changes that occur in the genital organs during sexual responses. The pelvic and hypogastric nerves relay through the major pelvic ganglion and the hypogastric plexus where the postganglionic neurons are located.

Lesley Marson, PhD, *is Associate Professor, Division of Urology, University of North Carolina, Chapel Hill.*

Top Spinal Cord Inj Rehabil 2002;8(1):42–50

Over the past three decades, many animal studies have examined the brain control of erection. However, few studies have been performed on the CNS control of female sexual responses. The majority of research has focused on the forebrain and peripheral mechanisms involved in hormonally regulated sexual behavior.[7–9] In animal models, lordosis is the most intensely studied female reproductive behavior. Although these studies have provided a great deal of knowledge related to hormone-dependent behavior,[8–10] they do not directly address genital responses. Moreover, the relationship between the lordosis reflex and human female sexual response is unclear, because humans do not display lordosis.

Beach[11] proposed that many components that integrate sexual behavior are generated in the hindbrain and spinal cord and that mechanisms for activating and organizing these components into a cognitive, integrative, and effective behavior are located in higher brain centers. Research to date has largely supported his theory. However, the brain and spinal cord neurons and pathways that normally inhibit and excite the various aspects of female sexual reflexes are still undefined. Genital reflexes, such as genital arousal and climax, are the products of spinal cord reflex mechanisms. These spinal circuits are modulated by brain inputs. Other pathways, such as sexual desire or proceptive behavior, may not be regulated by the spinal cord but may involve a spinal component.

Sensory (Afferent) Systems

The pudendal nerve mediates the sensory stimuli from the external genitals, the pelvic floor musculature, and surrounding areas including the perineum, clitoris, and urethra.[12–16] The sensory signals that relay through the pudendal nerve are essential for lordosis behavior[8,17] and the urethrogenital (UG) reflex, which is a reflex that mimics the nerve and muscle responses seen in human sexual climax.[18–20] The pudendal nerve afferents enter the spinal cord through the superficial dorsal horn of segments L6-S1, they then travel through the medial dorsal horn and enter the dorsal gray commissure, which is located in the medial cord (lamina X), where they terminate.[16,21]

The pelvic and hypogastric nerves mediate sensory information from the internal pelvic organs. Sensations to light touch, chemical stimuli, and noxious stimuli of the vagina, cervix, and uterus are mediated via the pelvic nerve.[22–25] Therefore, the pelvic nerve relays sensory information from genital manipulations during sexual behavior. The pelvic nerve is also crucial for the induction of pregnancy or pseudopregnancy due to mating or cervical stimulation.[26–28] Pelvic afferents terminate primarily in spinal segments L6-S1. The fibers course through the lateral dorsal horn and extend toward the intermediolateral cell column (IML). In addition, fibers course through the medial dorsal horn and enter the dorsal gray commissure.[29–31] The hypogastric afferents that innervate the uterus, cervix, and ovaries may be important in the transmission of noxious stimuli from the uterus.[24,32–34] The hypogastric nerve of the rat contains relatively few afferent fibers, which terminate in the medial dorsal horn and the dorsal gray commissure of spinal segments T13-L3.[21,29,35] Both the pelvic and the hypogastric nerve afferents are sensitive to the level of gonadal steroid hormones,[22,32–34] therefore, the intensity of sensory inputs depends on the stage of the estrus cycle.

Efferent (Output) Systems

The location of the spinal preganglionic neurons has been examined using retrograde tracers. Application of tracers to the rat pelvic nerve resulted in labeled cells in the parasympathetic preganglionic nucleus in the IML (also termed the sacral parasympathetic nucleus), primarily in L6-S1 of the spinal cord.[31,36] Application of tracers to the hypogastric nerve resulted in labeling of the sympathetic preganglionic neurons in T12-L1, primarily in L1-L2, of the spinal cord.[35,37,38] The majority of preganglionic neurons were found in the dorsal commissural nucleus with bilateral labeling in the IML.

The efferent fibers of the pudendal nerve provide innervation of the pelvic floor and anal and urethral sphincters.[16,39,40] The pudendal motoneurons are located in the ventral horn of L5-L6 of the spinal cord. The motoneurons are located in the ventral horn in Onuf's nucleus, which in the rat is divided anatomically into the dorsomedial and dorsolateral nuclei.

Spinal Interneurons

The afferents of the pelvic, hypogastric, and pudendal nerves enter the dorsal horn and terminate around the IML and/or dorsal gray commissure. The afferent neurons then synapse and relay through spinal interneurons, which eventually send signals to the efferent neurons that control the pelvic organs. The sensory information is also sent to other spinal segments and to the brain. Spinal autonomic and somatic afferents and efferents that regulate sexual function are located in spinal segments T12-L1 (sympathetic) and L5-S1 (parasympathetic and somatic). However, sensory inputs and motor output of the genital organs are not mediated independently, that is, sexual reflexes comprise an integration of autonomic and somatic responses. Therefore, the afferent and efferent branches of these nerves must send inputs to each other via spinal interneurons that transverse multiple spinal segments. A number of electrophysiological, anatomical, and functional studies have provided some information concerning the location of these spinal interneurons.

Anatomical transneuronal tracing studies using the neurotrophic virus, pseudorabies virus (PRV), have demonstrated the spinal neurons that innervate the pelvic organs.[41–44] This virus can be injected into a peripheral organ, where it is taken up by nerve endings and then retrogradely transported back to the cell body. The virus is then replicated and released at sites of synaptic contact. The virus is retrogradely transported to the cell body of the next neuron. In this way, the output (efferent) pathway, that is, the first, second, and third order neurons, that projects to a particular pelvic organ may be visualized.[45] PRV was injected into the clitoris and uterus of females rats.[42,44,45] First order neurons were found in the major pelvic ganglia. Second order neurons (preganglionic neurons) were found primarily in and around the IML in segments T12-L1 and L5-S1 and in the dorsal gray commissure of T13-L1. Spinal interneurons were located in the vicinity of the IML at these segments as well as in the dorsal gray commissure forming a column of neurons through segments T13-S1. A few spinal interneurons were also found in the intermediate gray. These studies suggest that spinal interneurons involved in sexual function course through the lower thoracic lumbosacral cord in the lateral gray and in the

dorsal gray commissure. These cells may be important in the integration of pelvic responses seen during sexual behavior.

Electrophysiological recordings in the cat have also shown the importance of interneurons in the medial spinal cord. The largest field potentials and greatest number of synaptically activated neurons were found in the medial portions of the lumbosacral spinal gray.[46] Spinal interneurons in the medial gray of the sacral spinal cord have also been isolated that respond to pelvic visceral and perineal stimulation.[47]

C-fos is an immediate early gene that can be visualized in activated neurons through the use of immunohistochemistry.[48,49] This technique has been used to identify spinal neurons that are activated during sexual function.[50,51] Stimulation of genital nerves and reflexes resulted in the labeling of neurons in the medial dorsal horn, in and close to the IML, and the dorsal gray commissure of spinal segments T12-S1. The distribution of fos-labelled neurons matched the location of the pelvic afferents and efferents as well as the labelled spinal interneurons mapped from anatomical tracing studies. Therefore, the dorsal gray commissure is important in mediating and integrating spinal cord genital reflexes. In addition, interneurons in the lateral gray, dorsal horn, and intermediate cord may be involved.

Ascending and Descending Spinal Pathways

The spinothalamic and spinoreticular pathways relay sensory information to the brain. These pathways primarily travel in the dorsal columns and dorsal lateral quadrant and consist primarily of fast myelinated fibers, which terminate in the thalamus.[51–53] Most of the spinoreticular fibers cross to the opposite side of the cord and travel in the lateral spinal columns and terminate in brainstem reticular formation. The sensory inputs cross the spinal cord below T8.[52] Descending information from the brain also passes through the dorsal and dorsolateral white matter before entering the spinal gray; the majority of the fibers of these pathways are crossed.

Spinal Reflexes

After SCI, a significant number of women are still able to experience genital vasocongestion and orgasm.[2,53] Complete SCI at T6 and above allows subjective arousal but not psychologically based genital arousal to occur[2,54]; in addition, SCI and upper motor neuron neurological dysfunction that affects the sacral spinal cord leads to preservation of the ability to achieve reflex genital vasocongestion.[2,54] By classifying women based on sensory preservation of their dermatomes, Sipski and colleagues[55] showed that differences in genital responses to audio-visual erotic stimulation were based on the degree of sensory damage in the T11-L2 dermatomes. The sympathetic nervous system afferents and efferents that innervate the genital organs relay in the spinal cord at these levels. Therefore, these data suggest that genital vasocongestion may be regulated by the sympathetic nervous system. Evidence that supports a facilitatory role for the sympathetic nervous system on genital arousal and subjective arousal has also been documented.[55–58]

Human studies have reported that orgasmic reflexes are still present after upper SCI.[2,53–55] Women with injury of S2-S5 dermatomes and the lower motor neurons are

less likely to reach orgasm through direct genital stimulation compared to women with injury of T11 and above.[55] These data suggest that orgasmic responses, in humans, require intact reflexes that relay in the sacral spinal cord. These data agree with the animal model in which "climactic" responses (i.e., UG reflex) can be elicited in anesthetized animals with complete spinal cord transections at T10 and above.[19,20,59]

The UG reflex is a sexual response in which reflex genital responses can be elicited in anesthetized animals. There is evidence that the UG reflex is generated by a multisegmental spinal pattern generator, which involves the coordination of sympathetic, parasympathetic, and somatic efferents innervating the genital organs.[20] Recordings in human females during orgasm have shown coordinated rhythmic contractions of the vagina and anal sphincter that are virtually identical to recordings obtained during the UG reflex in the female rat.[18,20] Due to the fact that sexual responses are bilaterally regulated, injury that is confined to one side of the spinal cord may preserve these reflexes. Moreover, human data have suggested that there is a differential control of genital vasocongestion and orgasm by different levels of the spinal cord and possibly different branches of the nervous system. Therefore, examination of the spinal circuits involved in genital arousal and orgasm in animal models may further elucidate and differentiate the spinal and brain pathways that regulate various female genital responses.

Sensory and efferent information related to genital responses may be relayed through the vagal nerve in addition to the spinal cord. Evidence has been documented suggesting that vagal fibers convey sensory information from female pelvic organs to sensory nuclei in the brainstem.[13,60,61] The vagal pathway remains functional after spinal cord transection and may account for the menstrual cramping, analgesia, and orgasm reported in women with complete spinal cord transections.[62,63] Thus, the vagal pathway may be supplemental to the spinal systems. The vagal pathway may act to facilitate excitatory influences of information from the reproductive organs, which may be important after SCI.[60] However, further animal studies and verification of this hypothesis in clinical studies is required.

Summary

There is medical evidence that sexual responses, including climax, can be activated in the cervical or thoracic spinal cord-injured patient, and thus the lower spinal cord has the necessary circuitry to mediate sexual responses.[3] Anatomical studies suggest that the spinal control of genital organs that comprise genital arousal and climax can be regulated as follows. Figure 1 shows a summary of these pathways. Afferent genital information via sensory nerve fibers would be relayed from the genital organs through the pelvic and pudendal nerves and would enter the dorsal horn of the lumbosacral spinal cord. The dorsal horn neurons then would relay their inputs to spinal interneurons that are located in the medial cord (lamina X) and in the vicinity of the preganglionic and motoneurons in the IML and ventral horn of the lumbosacral spinal cord. Efferent output that mediates muscular contractions would then be regulated via the parasympathetic and sympathetic preganglionic neurons that innervate the vagina, clitoris, urethra, and uterus and the motor neurons that innervate the anal sphincter and pelvic floor muscles.

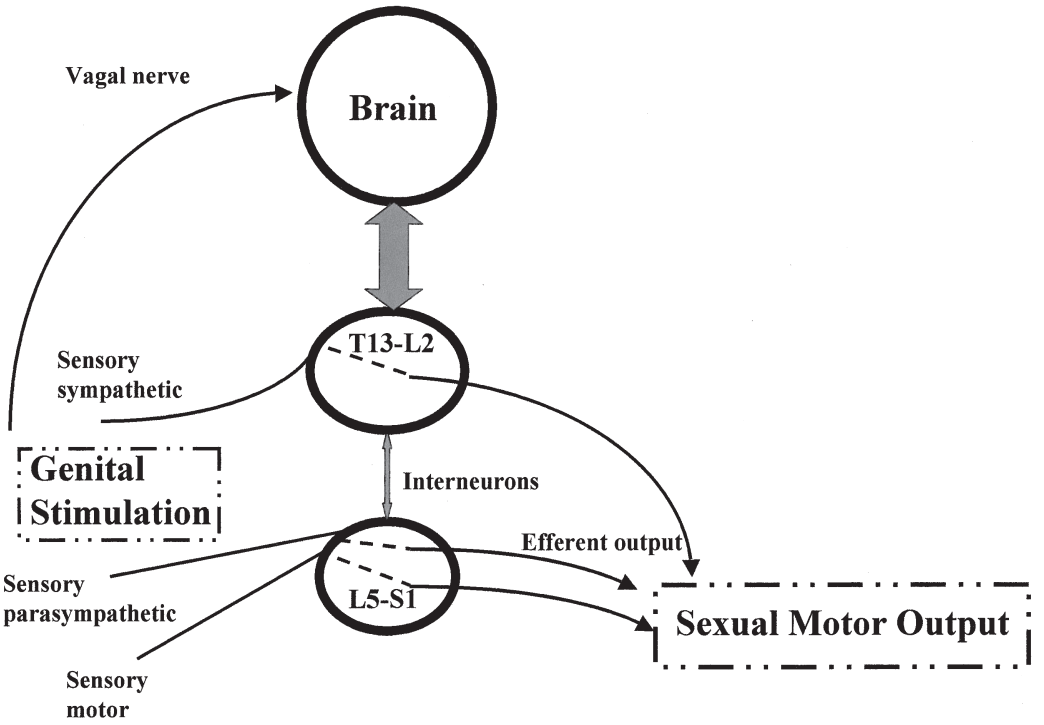

Figure 1. Diagrammatic representation of the afferent (sensory) and efferent pathways that regulate genital reflexes. Dashed lines in the spinal cord represent interneuronal pathways, and the arrow connecting the spinal segments, T13-L2 and L5-S1, represents spinal interneurons that are present throughout segments T13-S1. Genital sensory information is relayed in the autonomic (sympathetic and parasympathetic) and motor (pudendal) nerves and enters the spinal cord. Interneurons then relay messages through the spinal cord within and through multiple spinal segments. These signals may also be sent to the brain. The efferent output then coordinates the appropriate sexual motor output, for example, climax. The vagal nerve may send sensory information directly to the brain.

These spinal circuits are found in T13-S1. Therefore, injury above T12 should preserve the ability to achieve genital arousal and climax. Spinal damage of the lower lumbosacral cord may disrupt the physiological reflexes that comprise climax. Sensory perception of changes in the pelvic organs may remain intact due to a pathway that utilizes the vagus nerve. CNS pathways that regulate sexual desire and cognitive arousal are presently unknown.

Acknowledgments

This work was funded by National Institute of Health grant NS39166.

REFERENCES

1. Black K, Sipski ML, Strauss SS. Sexual satisfaction and sexual drive in spinal cord injured women. *J Spinal Cord Med.* 1998;21:240–244.
2. Sipski ML, Alexander CJ, Rosen RC. Orgasm in women with spinal cord injuries: A laboratory-based assessment. *Arch Phys Med Rehabil.* 1985;76:1097–1102.
3. Sipski ML, Craig AJ, Rosen RC. Physiological parameters associated with sexual arousal in women with incomplete spinal cord injuries. *Arch Phys Med Rehabil.* 1997;78:305–313.
4. Baljet B, Drukker J. The extrinsic innervation of the pelvic organs in the female rat. *Acta Anat.* 1980;107:241–267.
5. Bell C. Autonomic nervous control of reproduction: Circulatory and other factors. *Pharm Rev.* 1972;24:657–736.
6. Jänig W, McLachlan EM. Organization of lumbar spinal outflow to distal colon and pelvic organs. *Physiol Rev.* 1987;67:1332–1403.
7. Frohlish J, Morgan M, Ogawa S, Burton L, Pfaff D. Statistical analysis of measures of arousal in ovariectomized female mice. *Horm Behav.* 2001;39:39–47.
8. Pfaff DW, Schwartz-Giblin S. Cellular mechanisms of female reproductive behaviors. In: Knobil E, Neill J, eds. *The Physiology of Reproduction.* New York: Raven Press; 1988,1487–1568.
9. Rose JD. Brainstem influences on sexual behavior. In: Klemm WR, Vertes RP, eds. *Brainstem Influences on Sexual Behavior.* New York: John Wiley; 1990:407–463.
10. Erskine MS. Solicitation behavior in the estrous female rat: A review. *Horm Behav.* 1989;23(4):473–502.
11. Beach FA. Cerebral and hormonal control of reflexive mechanisms involved in copulatory behavior. *Physiol Rev.* 1967;47:289–316.
12. Adler NT, Davis PG, Komisaruk BR. Variation in the size and sensitivity of a genital sensory field in relation to the estrous cycle in rats. *Horm Behav.* 1977;9:334–344.
13. Komisaruk BR, Adler NT, Hutchinson J. Genital sensory field: Enlargement by estrogen treatment in female rats. *Science.* 1972; 178:1295–1298.
14. Kow L-M, Pfaff DW. Effects of estrogen treatment on the size of receptive field and response threshold of pudendal nerve in the female rat. *Neuroendocrinol.* 1973;13:299–313.
15. Langworthy OR. Innervation of the pelvic organs of the rat. *Invest Urol.* 1965;2:491–511.
16. McKenna KE, Nadelhaft I. The organization of the pudendal nerve in the male and female rat. *J Comp Neurol.* 1986;248:532–549.
17. Pfaff DW. *Estrogens and Brain Function.* New York: Springer-Verlag; 1980.
18. Bohlen JG, Held JP, Sanderson MO, Ahlgren A. The female orgasm: Pelvic contractions. *Arch Sex Behav.* 1982;11:376–386.
19. Chung SK, McVary KT, McKenna KE. Sexual reflexes in male and female rats. *Neurosci Lett.* 1988;94:343–384.
20. McKenna KE, Chung SK, McVary KT. A model for the study of sexual function in anesthetized male and female rats. *Am J Physiol.* 1991;261:R1276–1285.
21. Thor KB, Morgan C, Nadelhaft I, Houston M, de Groat WC. Organization of afferent and efferent pathways in the pudendal nerve of the female cat. *J Comp Neurol.* 1989;288:263–279.
22. Berkeley KJ, Robbins A, Sato Y. Functional differences between afferent fibers in the hypogastric and pelvic nerves innnervating female reproductive organs in the rat. *J Neurophysiol.* 1993;69:533–543.
23. Berkley KJ, Hotta H, Robbins, A, Sato Y. Functional properties of afferent fibers supplying reproductive and other pelvic organs in pelvic nerve of female rat. *J Neurophysiol.* 1990;63:256–272.
24. Berkeley KJ, Wood E, Scofield SL, Little M. Behavioral responses to uterine or vaginal distension in the rat. *Pain.* 1995;61:121–131.
25. Peters LC, Kristal MB, Komisaruk BR. Sensory innervation of the external and internal genitalia of the female rat. *Brain Res.* 1987;408:199–204.
26. Carlson RR, De Feo VJ. Role of the pelvic nerve vs. the abdominal sympathetic nerves in the reproductive function of the female rat. *Endocrinol.* 1965;77:1014–1022.
27. Kollar EJ. Reproduction in the female rat after pelvic neurectomy. *Anat Rec.* 1953;115:641–658.
28. Traurig HH, Papka RE, Rush ME. Effects of capsaicin on reproductive function in the female rat: Role of peptide-containing primary afferent nerves innervating the uterine cervix in the neuroendocrine copulatory response. *Cell Tiss Res.* 1988;253:573–581.

29. Morgan C, Nadelhaft I, de Groat WC. The distribution of visceral primary afferents from the pelvic nerve to Lissauer's tract and the spinal gray matter and its relationship to the sacral parasympathetic nucleus. *J Comp Neurol.* 1981;201:415–440.
30. Nadelhaft I, Roppolo J, Morgan C, de Groat WC. Parasympathetic preganglionic neurons and visceral primary afferents in monkey sacral spinal cord revealed following application of horseradish peroxidase to pelvic nerve. *J Comp Neurol.* 1983;216:36–52.
31. Nadelhaft I, Booth AM. The location and morphology of preganglionic neurons and the distribution of visceral afferents from the rat pelvic nerve: A horseradish peroxidase study. *J Comp Neurol.* 1984;226:238–245.
32. Berkley KJ, Robbins A, Sato Y. Uterine afferent fibers in the rat. In: Schmidt RF, Schaible H-G, Vahle-Hinz C, eds. *Fine Afferent Nerve Fibers and Pain.* Weinheim: VCH Verlag, 1987:129–136.
33. Berkley KJ, Robbins A, Sato Y. Afferent fibers supplying the uterus in the rat. *J Neurophysiol.* 1988;59:142–163.
34. Robbins A, Sato Y, Hotta H, Berkley, KJ. Responses of hypogastric nerve afferent fibers to uterine distension in estrous or metestrous rats. *Neurosci Lett.* 1990;110:82–85.
35. Nadelhaft I, McKenna KE. Sexual dimorphism in sympathetic preganglionic neurons of the rat hypogastric nerve. *J Comp Neurol.* 1987;256:308–315.
36. Hancock MB, Peveto CA. Preganglionic neurons in the sacral spinal cord of the rat: An HRP study. *Neurosci Lett.* 1979;11:1–5.
37. Hancock MB, Peveto CA. A preganglionic autonomic nucleus in the dorsal gray commissure of the lumbar spinal cord of the rat. *J Comp Neurol.* 1979;183:65–72.
38. Neuhuber W. The central projections of visceral primary afferent neurons of the inferior mesenteric plexus and hypogastric nerve and the localization of the related sensory and preganglionic sympathetic cell bodies in the rat. *Anat Embryol.* 1982;163:413–425.
39. Breedlove SM, Arnold AP. Hormone accumulation in a sexually dimorphic motor nucleus of the rat spinal cord. *Science.* 1980;210:564–566.
40. Schrøder HD. Organization of the motoneurons innervating the pelvic muscles of the male rat. *J Comp Neurol.* 1980;192:567–587.
41. Marson L. Central nervous system neurons identified after injection of pseudorabies virus into the rat clitoris. *Neurosci Lett.* 1995;190: 41–44.
42. Marson L. Identification of CNS neurons that innervate the bladder and urethral sphincter in female rats. *J Comp Neurol.* 1997;389:584–602.
43. Papka RE, McCurdy JR, Williams SJ, Mayer B, Marson L, Platt KB. Parasympathetic preganglionic neurons in the spinal cord involved in uterine innervation are cholinergic and nitric oxide-containing. *Anat Rec.* 1995;241:554–562.
44. Papka RE, Williams S, Miller KE, Copelin T, Puri P. CNS location of uterine-related neurons revealed by trans-synaptic tracing with pseudorabies virus and their relation to estrogen receptor-immunoreactive neurons. *Neurosci.* 1998;84:935–952.
45. Card JP, Rinaman L, Lynn RB, Lee BH, Meade RP, Miselis RR, Enquist LW. Pseudorabies virus infection of the rat central nervous system: Ultrastructural characterization of viral replication, transport and pathogenesis. *J Neurosci.* 1993;13:2515–2539.
46. Fedirchuk B, Song L, Downie JW, Shefchyk SJ. Spinal distribution of extracellular field potentials generated by electrical stimulation of pudendal and perineal afferents in the cat. *Exp Brain Res.* 1992;89:517–520.
47. Honda CN. Visceral and somatic afferent convergence onto neurons near the central canal in the sacral spinal cord of the cat. *J Neurophysiol.* 1985;11:1059–1076.
48. Birder LA, Roppolo JR, Ladarola MJ, de Groat WC. Electrical stimulations of visceral afferent pathways in the pelvic nerve increase c-fos in the rat lumbosacral spinal cord. *Neurosci Lett.* 1991;129:193–196.
49. Dragunow M, Faull R. The use of c-fos as a metabolic marker in neuronal pathway tracing. *J Neuro Meth.* 1989;29:261–265.
50. Lee JW, Erskine MS. Vaginocervical stimulation suppresses the expression of c-fos induced by mating in thoracic, lumbar and sacral segments of the female rat. *Neurosci.* 1996;74:237–249.
51. Rampin O, Gougis S, Giuliano F, Rousseau JP. Spinal fos labeling and penile erection elicited by stimulation of dorsal nerve of the rat penis. *Am J Physiol.* 1997;272:R1425–R1431.
52. Hubscher CH, Johnson RD. Effects of acute and chronic midthoracic spinal cord injury on neural circuits for male sexual function. I.

Ascending pathways. *J Neurophysiol.* 1999;82:1381–1889.
53. Bors E, Comarr AE. Neurological disturbances of sexual function with special reference to 529 patients with spinal cord injury. *Urol Survey.* 1960;10:191–222.
54. Sipski ML, Alexander CJ, Rosen R. Physiological parameters associated with sexual arousal in women with incomplete spinal cod injuries. *Arch Phys Med Rehabil.* 1995;76:1097–1102.
55. Sipski ML, Alexander CJ, Rosen R. Sexual arousal and orgasm in women: Effect of spinal cord injury. *Ann Neurol.* 2001;49:35–44.
56. Meston CM, Gorzalka BB. The differential effect of sympathetic activation on sexual arousal in sexually functional and dysfunctional women. *J Abnorm Psychol.* 1996;4: 143–148.
57. Palace EM, Gorzalka BB. The enhancing effect of anxiety on arousal in sexual dysfunctional and functional women. *J Abnorm Psychol.* 1990;99:403–411.
58. Meston CM, Heiman JR. Ephedrine activated physiological sexual arousal in women. *Arch Gen Psychiatry.* 1998;55:652–656.
59. Vathy I, Marson L. Effects of prenatal morphine and cocaine on sexual reflexes in male and female rats. *Physiol Behav.* 1998;63:445–450.
60. Hubscher CH, Berkely KJ Spinal and vagal influences on the response of rat solitary nucleus neurons to stimulation of uterus, cervix and vagina. *Brain Res.* 1995;702:251–254.
61. Komisaruk BR, Gerdes CA, Whipple B. "Complete" spinal cord injury does not block perceptual responses to genital self-stimulation in women. *Arch Neurol.* 1997;54:1513–1520.
62. Whipple B, Richards E, Tepper M, Komisaruk BR. Sexual responses in women with complete spinal cord injury. In: Krotosku DM, Nosek M, Turk M, eds. *The Health of Women with Physical Disabilities: Setting a Research Agenda for the 90s.* Baltimore, MD: Paul H. Brookes; 1995.
63. Whipple B, Gerdes CA, Komisaruk BR. Sexual response to self-stimulation in women with complete spinal cord injury. *J Sex Res.* 1996;33:231–240.