Behavioral and Physiological Evidence of Sexual Climax in the Female Stump-Tailed Macaque (*Macaca Arctoides*)

Abstract. *Intense tonic/clonic uterine contractions and sudden increases in heart rate coincided with the behavioral homolog of a male ejaculatory response (minus seminal emission) in a normal female stump-tailed macaque engaged in homosexual mounting episodes. The behavioral patterns were also observed in four of ten females during 5 to 40 percent of heterosexual copulations. These observations demonstrate the existence of an orgasmic response in a nonhuman primate.*

Orgasm in women is defined as an intense sexual response consisting of (i) a specific subjective experience, (ii) a set of overt behavioral responses, and (iii) physiological changes including stereotyped patterns of uterine contraction and sudden heart rate increase (*1*). In spite of earlier opinions to the contrary (*2*), the question of whether female nonhuman primates can display an orgasmic behavioral pattern during episodes of heterosexual or homosexual activity has been reopened (*3, 4*).

Much of the evidence suggestive of sexual climax in female nonhuman primates has been limited to observations of sudden behavioral changes that occur concomitantly with the male's ejaculation, such as a staccato grunting by female Chacma baboons (*5*) or a reaching back and clutching reaction of female rhesus monkeys (*6*). Three studies have dealt with the measurement of physiological changes during sexual stimulation in nonhuman primates (*7-9*). None of these studies has resulted in an unambiguous resolution of the question of orgasm, although excitement, plateau, and resolution phases were described in one study based on heart rate and vulval/clitoral color changes (*7*). In another study, heart rate changes of females coincident with their male partners' ejaculations were distinct and possibly analogous to patterns shown by women at orgasm (*9*). Uterine contractions during coitus have not shown an orgasmic pattern, however (*8*).

For rhesus and stump-tailed macaques, homosexual episodes are described in two studies in which females performed mounts and a series of pelvic thrusts to a female partner, and then displayed the behavioral homolog of the entire species-typical male ejaculatory pattern (*10, 11*). This kind of evidence from the stump-tailed macaque is noteworthy, since the ejaculatory response is distinctive in that species, including not only body tenseness and rigidity, but also a characteristic round-mouthed facial expression shown together with repeated vocalized expirations (*10, 12*). That the female had control of the genital stimulation she received in these homosexual interactions was undoubtedly relevant to the regular occurrence of the response. In spite of their similarity to the male's behavior at ejaculation, even these observed responses are not sufficient to resolve the question of orgasm without additional confirmatory evidence from physiological measures.

We used six adult female stump-tailed macaques; they were individually housed at the Netherlands Primate Center (TNO, Rijswijk, Holland) and cared for as described (*13*). Behavioral testing was conducted by transporting animals to a wire mesh cage (1.7 by 1.7 by 2.5 m) equipped with two large interior platforms and a Plexiglas front. The cage was modified to facilitate radio telemetric recordings by electrically isolating its wire grid floor, thus allowing the entire enclosure to be used as an antenna. Sexual behavior sequences [defined in (*12*)] were recorded by an SSR event recording system (*14*).

Tests were given by placing the six females together in the observation cage. This procedure, repeated four times over a 2-week period, produced in each instance a flurry of aggression followed by a mounting series between the most dominant female and one particular partner. The mounts which were performed in a seated ventral-dorsal position culminated with a 20- to 45-second display of an ejaculatory-like pattern by the mounter, including the round-mouthed "ejaculation face" and its associated vocalizations. The female receiving the mount reacted to her partner's sudden change in behavior by lip-smacking, looking back, reaching back, clutching her, and then kissing her—elements typically displayed by females of this species simultaneously with a male's ejaculation (*10, 15*).

The female with the highest prevalence of the behavioral homolog of the male ejaculatory pattern was then implanted with three separate battery-powered FM transmitters operating at 100 to 108 MHz: two to monitor uterine contractions, and one to record heart rate. The ECG (electrocardiogram) transmitter was placed subcutaneously in the epigastric region with its two electrodes 120 mm apart on the thoracic wall. Uterine contractions were measured with extraluminal force transducers as described (*16*) except that semiconductor

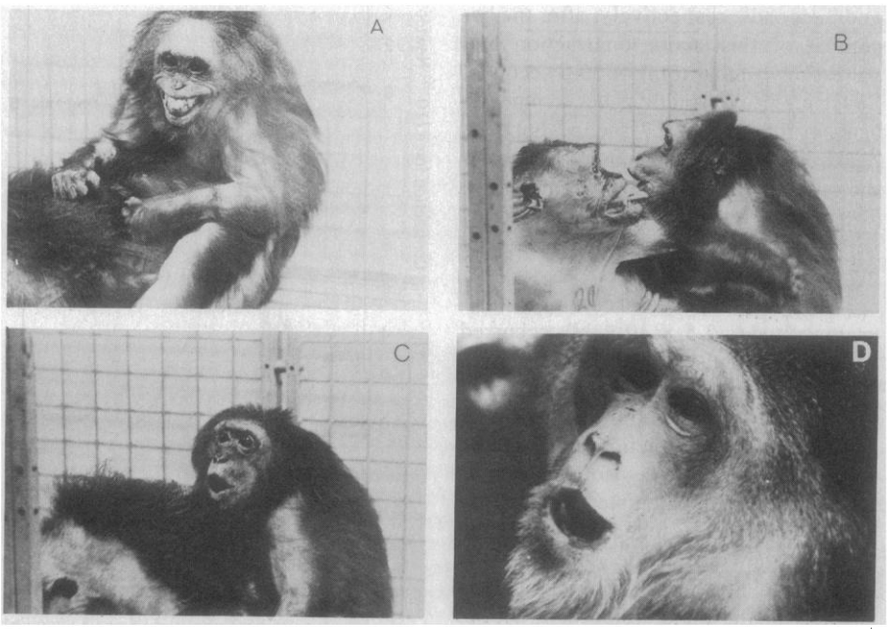

Fig. 1. (A-C) Sequence of facial expressions by a female engaged in a homosexual mount. (A) Grin-lip-smacking. This pattern was displayed through most of the mount and was not associated with major uterine activity or heart rate changes. (B) Display of the round-mouthed "ejaculation face" by the mounting female. Major uterine contraction and heart rate acceleration were associated with this behavior. At the same time, the female partner reacted to this behavioral pattern by displaying look back, reach back, and kiss. (C) Continuation of the round-mouthed expression. (D) The round-mouthed expression of a male stump-tail macaque shown coincident with his ejaculation.

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strain gauges embedded in silastic were used (*17*). The ECG and uterine force signals together with the SSR behavioral event recording system output were directly monitored on oscilloscopes and were recorded with a multichannel instrumentation tape recorder for further analysis.

Seven days after receiving the implantation, the female was placed alone in the observation cage on each of three consecutive days for 5 to 10 minutes and then the other five females were introduced into the cage with her. On two of these three test days, the implanted female mounted her favorite partner and thrusted while continuously lip-smacking until the round-mouthed ejaculation face was displayed (Fig. 1). The response was accompanied by piloerection, body tenseness, rhythmic vocalized expirations, and then ended abruptly with generalized muscular relaxation. The uterine contraction pattern that occurred with the ejaculatory facial expression is shown in Fig. 2C. Records of uterine contractions during the receipt of genital grooming and during a mount series that did not culminate in the ejaculatory-like pattern are shown in Fig. 2, A and B, respectively. An intense (7.7×10^{-2} N) sustained tonic uterine contraction developed 8 to 10 seconds prior to the overt behavioral changes and continued for 50.0 seconds. Piloerection and the "ejaculation face" were displayed 7 and 9 seconds, respectively, after the beginning of this major contraction and were shown for a total of 30.0 seconds. Seven clonic contractions occurring with a mean interval of 0.7 second between peaks were measured 6.0 seconds after the onset of the major tonic contraction. The uterus returned to baseline tonus within 10 seconds after the female ended her facial expression.

Three additional contractions of smaller magnitude (2.5×10^{-2} N) occurred within 10 seconds of the end of the main contraction, and then a presumed loss of uterine tonus (a deflection of 8.0×10^{-2} N in the negative direction) occurred 90 seconds later and lasted for 40 seconds more. Heart rate, calculated for each 10-second interval, changed abruptly from 186 beat/min during the course of the mount to 210 beat/min within the first 10 seconds of the major tonic contraction. Heart rate had never exceeded 192 beat/min at any other time in the study, even during intense agonistic encounters. Heart rate then progressively slowed down and stabilized to 186 beat/min by the end of the tonic contraction. The second recorded orgasmic incidence, observed the following day, had essentially the same characteristics of a single major tonic contraction lasting 40 seconds and measured at 6.8×10^{-2} N maximum force, followed in this instance within 5 seconds by a 40-second period of uterine relaxation. Again, the major tonic contraction was displayed simultaneously with the behavioral pattern. No instance of contractions of these forces or durations were seen under other conditions of testing, although minor contraction-pattern changes were detected and appeared to be related to either genital stimulation or social conditions (see Fig. 2A).

In a separate study with other stump-tailed macaques, ten intact females and five intact males were observed in heterosexual pair tests of 20 minutes duration on alternate days for two 40-day periods. In addition to certain behavioral data already reported (*15*), we observed that four of ten intact females displayed the round-mouthed response during at least one copulatory episode with a mean frequency of 9.8 per female based on an average of 52 tests each. No clear relation of the response to any particular phase of the cycle was observed. Marked individual differences were noted, however, with one female displaying the response on nearly 40 percent of copulations.

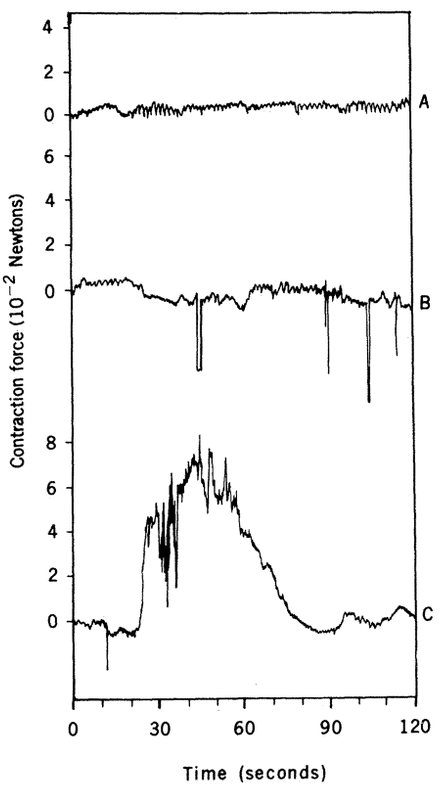

Fig. 2. Uterine contraction records of a female stump-tailed macaque during (A) receipt of genital grooming, (B) execution of a mount which did not terminate with the round-mouth expression, and (C) execution of a mount in which the round-mouth expression was displayed. All sequences were recorded during the same test. The abrupt transient decreases in contraction force seen in (B) are movement artifacts.

There is obviously no way to measure or compare the subjective sensory experience associated with the response in stump-tailed macaques with that of the human experience. However, we believe that the physiological events described are similar to those recorded for women at orgasm. The extent to which this response might influence sexual motivation and other aspects of reproduction remains to be determined. The clear demonstration of an orgasmic phenomenon in simian primates has immediate applications to studies on the evolution of human behavior (*18*).

D. A. GOLDFOOT*
H. WESTERBORG-VAN LOON
W. GROENEVELD
A. KOOS SLOB
Departments of Endocrinology, Growth and Reproduction and
Medical Technology, Faculty of Medicine, Erasmus University, Rotterdam, The Netherlands

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17. The transducers (10 by 20 by 3 mm) were sutured transversely on the ventral surface of the uterus, one just below the fundus and the other near the uterocervical junction, with the transmitters placed in the abdominal cavity. An FM-FM system was employed to code slow tonic uterine contractions wherein variations in resistance caused by distortion of the force transducer resulted in frequency modulation of a subcarrier oscillator that in turn modulated the carrier frequency of the transmitter.
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19. We thank W. Kort and J. Dortland for surgical assistance, J. Loeve for computer services, and J. V. Baker and P. Schenck for technical support; H. Koning and his staff at the TNO primate center for animal care services: J. J. van der Werff ten Bosch for support and encouragement of the project. D.A.G. was funded by a visiting scientists program of the Rotterdam Medical Faculty, and expresses appreciation to that institution. Supported in part by NIH grant RR00167.
* Present address: Wisconsin Regional Primate Research Center, 1223 Capitol Court, Madison 53706.

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Leucine Enkephalin: Localization in and Axoplasmic Transport by Sacral Parasympathetic Preganglionic Neurons

Abstract. *Nerve processes and cell bodies containing leucine enkephalin were demonstrated in the sacral autonomic nucleus of the cat by immunocytochemical methods. Enkephalinergic preganglionic perikarya were seen only when axonal transport was blocked either by colchicine or by ventral root ligation. Ligation of the sacral ventral roots also produced damming of enkephalin immunoreactivity proximal to the S_2 ligature. These data indicate that parasympathetic preganglionic neurons synthesize and transport enkephalin or enkephalin-like immunoreactive compounds to the periphery.*

In the cat, the smooth musculature of the pelvic viscera receives its innervation indirectly from parasympathetic preganglionic neurons of the sacral spinal cord. The majority of these cells are located along the lateral border of the intermediate and ventral gray matter of S_2 and upper S_3 (*1–5*). In contrast, striated pelvic sphincter muscles are innervated by a column of motor neurons in the ventral horn, which extends from S_1 to upper S_2 (*3*). These neurons form the feline homolog of the motor column of Onuf (*6*). In light of previous studies that demonstrated enkephalin in the rat autonomic nervous system and our observations of enkephalin in the feline dorsal motor nucleus of the vagus (*7*), we sought to determine whether the influence of opiates on pelvic visceral reflexes (*8*) indicates an endogenous opioid preganglionic innervation. Our results indicate that sacral parasympathetic preganglionic neurons of the spinal cord synthesize the endogenous opiate receptor ligand leucine enkephalin ([Leu]enkephalin) and transport it intra-axonally to the periphery.

We used immunocytochemical techniques to identify [Leu]enkephalin in both the sacral spinal cord and sacral ventral roots. Untreated and colchicine-treated cats were perfused via the aorta sequentially with 200 ml of 0.1*M* phosphate buffer, 2 liters of 4 percent paraformaldehyde in 0.1*M* phosphate buffer or the same fixative containing 0.2 percent glutaraldehyde, and finally with 500 ml of 0.1*M* phosphate buffer. Sacral segments S_1 to S_3 and the appropriate sacral roots were dissected, dehydrated, and embedded in paraffin. Leucine enkephalin was localized on 20-μm paraffin or 50-μm Vibratome sections by the unlabeled antibody peroxidase-antiperoxidase technique (*9*) with specific antiserum to [Leu]enkephalin conjugated to keyhole limpet hemocyanin (*10*). To control for antibody specificity, adjacent sections were incubated with [Leu]enkephalin antiserum (diluted 1:1000) that had been preabsorbed with an excess of [Leu]-enkephalin [100 μg of [Leu]enkephalin (Boehringer-Mannheim) per milliliter of antiserum]. Results of all control studies were negative.

In the sacral cord of untreated animals we found no enkephalinergic cell bodies. Enkephalin-like immunoreactivity in nerve processes was most densely concentrated in the superficial dorsal horn (laminae I and II), in the intermediate gray matter, and around the central canal (Fig. 1, A and B). In the second sacral segment, enkephalin staining was more intense along the ventrolateral border of the gray matter and adjacent lateral funiculus (Fig. 1B). This area corresponds to the intermediolateral sacral autonomic nucleus (*1–3*). Thin varicose enkephalin-containing processes were scattered throughout the sacral ventral horn. The motor column of Onuf, however, contained a rich plexus of enkephalinergic processes throughout its rostral-caudal extent (S_1 to rostral S_2) (Fig. 1A). This dense pattern of enkephalin immunoreactivity in the Onuf nucleus suggests that exogenous opiates exert a direct spinal action on somatic motor neurons of the viscera.

The distribution of sacral enkephalin perikarya was studied in two cats pretreated with colchicine. Twenty micrograms of colchicine (Sigma) dissolved in 2 μl of sterile saline was injected into the spinal cord at the L_7-S_1 junction. In addition, a pledget of Gelfoam (Upjohn) saturated with colchicine (100 μg/μl) was placed directly over the dorsal surface of spinal segments S_1 to S_3. The wound was sutured with the Gelfoam in place, and the animals were killed 17 to 48 hours later.

Two groups of labeled enkephalin perikarya appeared in the intermediate gray matter of S_2 to S_3 in the colchicine-treated animals (Fig. 1C). The distribution and morphology of these cells were strikingly similar to those of the sacral parasympathetic preganglionic neurons (*1–3*) in the cat, identified either by chromatolysis or by retrogradely transported

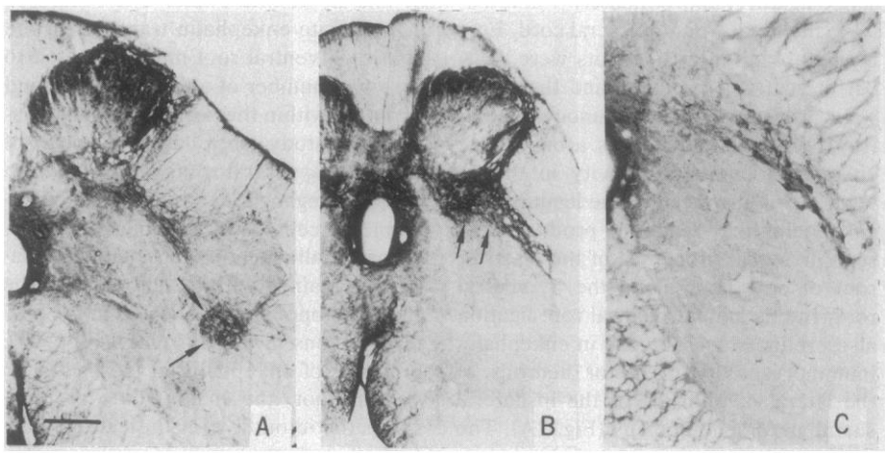

Fig. 1. Immunocytochemical localization of [Leu]enkephalin in the S_1 (A) and S_2 (B and C) sacral spinal cord of the cat. In untreated spinal cord, enkephalin-immunoreactive nerve processes are concentrated in the superficial dorsal horn, intermediate gray matter, and around the central canal. No enkephalin cell bodies are labeled. Arrows point to dense reaction product in the motor column of Onuf (A) and sacral autonomic nucleus (B). In colchicine-treated cord (C), numerous enkephalin perikarya appear in the sacral autonomic nucleus. Scale bar is 1 mm in (A) and (B) and 400 μm in (C).

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