Penile pressures and muscle activity associated with erection and ejaculation in the dog

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Purowhit, Ram C., and Sidney D. Beckett. Penile pressures and muscle activity associated with erection and ejaculation in the dog. Am. J. Physiol. 231(5): 1343-1348. 1976.—A needle-tipped polyvinyl catheter or subminiature pressure transducer was implanted in the corpus cavernosum penis (CCP), corpus spongiosum penis (CSP), or bulbus glandis to determine the pressure during coitus in 42 dogs. Silver ring electrodes were implanted in the ischiocavernosus (IC) and bulbospongiosus (BS) muscles to monitor the electromyographic (EMG) activity of these muscles. The CCP pressure increased from 26 mmHg in the quiescent state to 161 mmHg at mild erection of the penis in the presence of a receptive female. During the intromission phase of coitus, the mean peak CCP pressure was 5,296 mmHg in the dogs with implanted catheters and 7,434 mmHg in the dogs with implanted transducers. The CCP pressure peaks during intromission were more in phase with the contractile activity of the IC muscles than with the BS muscles. Anesthesia of IC muscles with lidocaine significantly reduced the CCP pressures and the dogs with low pressures were unable to copulate because of insufficient erection for intromission, which indicated that the IC muscles were the source of energy for the high CCP pressure. The mean peak CSP and bulbus glandis pressures during the intromission phase of coitus were 579 and 1280 mmHg, respectively. The contractile activity of the BS muscles was in phase with the CSP pressure peaks. Anesthesia of BS muscles with lidocaine reduced the peak CSP and bulbus glandis pressures during attempted coitus. The mean rupture pressure of the CCP was 86,615 mmHg.

corpus cavernosum penis; corpus spongiosum penis; bulbus glandis; electromyography of penile muscles

The erectile pattern of the dog differs from man and most domestic animals in that there is a delayed engorgement of the bulbus glandis that results in the animals being locked together during mating for a period of 10–30 min. The dog also has an os penis and small corpus cavernosum penis (CCP) that become erect so that the dog can obtain intromission. The actual mechanism involved in maintaining turgescence of CCP, the corpus spongiosum penis (CSP), and the bulbus glandis during coitus has not yet been adequately elucidated for the dog. Beckett et al. (2) stated that erection was primarily due to increased pressure in the CCP of the horse; however, Christensen (8) and Hart (11) reported that erection in the dog was primarily due to the engorgement of the CSP, whereas Henderson and Roepke (14) stated that the CCP was probably the most important.

Some investigators proposed that increased blood flow into the penis was the main cause of erection, and constriction of venous drainage played little or no role in the erection (9, 16). Newman et al. (16) reported that during normal erection in man blood flow to the penis increased and venous restriction was not necessary and probably did not occur. Dorr and Brody (9) proposed that in the dog obstruction of venous drainage played little or no role in the erection process and the erection appeared to be produced by a large decrease in penile arterial resistance, resulting in an increased penile blood flow to facilitate the erection. Hart (11) also reported that obstruction of venous drainage was not essential for erection, but was essential for rapid engorgement of the bulbus glandis.

The CCP pressure in the anesthetized dog was measured by Henderson and Roepke (14) during erection produced by electrical stimulation of the nerves to the penis. They reported that the pressures in the CCP and carotid artery were approximately equal. Beckett et al. (2, 3, 7) reported that CCP pressure was much greater than the systemic arterial pressure during coitus. This significant increase in CCP pressure was correlated with intense increased activity of the ischiocavernosus (IC) muscles.

The electromyographic (EMG) activity of some external penile muscles has been studied in man (15), dog (11, 13), goat (3, 5), stallion (2), and bull (7) during erection and ejaculation. Hart and Kitchell (13) investigated the EMG activity of the IC, bulbospongiosus (BS), and ischiourethralis (IU) muscles in the dog while mechanically stimulating various areas of the penis. Hart (11) suggested that the IC muscles did not have an important role in facilitating erection in the dog. However, in the goat (3), stallion (2), and bull (7), it has been shown that anesthesia of the IC muscles with lidocaine usually prevented these animals from copulating due to inability to obtain erection. Kollberg et al. (15) demonstrated in the human that erection could occur without participation of the BS muscles. Watson (18) proposed in the bull and ram that under sexual stimulation the IC muscles contract, compressing the crura and forcing blood into the vessels of the CCP until the pressure is equal to arterial pressure. Hart (11, 13) reported that the contraction of the IU muscles, which insert on the fibrous ring encircling the common trunk of the left and right dorsal veins of the penis, was the mechanism to occlude venous return and facilitate the engorgement of the bulbus glandis.

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The magnitude of CSP and bulbous glandis pressures associated with coitus and ejaculation has not been determined in the dog. The CSP pressure in goat (4) and stallion (1) has been reported to be produced by contraction of BS muscles. It has been proposed that the contraction of BS muscles aids the forceful expulsion of the semen during ejaculation in goat (4), stallion (1), and dog (11, 13).

The present study was undertaken to define the role of external penile muscles and their effect on the CCP, CSP, and bulbous glandis pressure during erection and ejaculation in the actual process of copulation.

MATERIALS AND METHODS

Forty-two healthy male mongrel dogs were used in this study. The dogs were placed in four groups: group I (22 dogs), for implantation of a needle-tipped polyvinyl catheter in the CCP; group II (7 dogs), for implantation of a subminiature pressure transducer in the CCP; group III (7 dogs), for implantation of subminiature transducer in the bulbous glandis; and group IV (6 dogs), for implantation of a catheter in the CSP for pressure measurements during breeding. All dogs were implanted with a pair of silver ring electrodes in the IC and BS muscles for recording EMG activity during the breeding experiments.

The recording instrumentation was implanted at the sites shown in Fig. 1. The surgical procedure was as described by Beckett et al. (3). The dogs were anesthetized with pentobarbital sodium (30 mg/kg) and an endotracheal tube was inserted in the trachea to facilitate breathing during surgery. The dogs were placed on a surgical table in left or right lateral recumbency. The penis and IC and BS muscles were exposed by a midline incision in the perineal region. The polyvinyl catheter or transducer cable and plastic-coated EMG lead wires were routed subcutaneously and exteriorized near the base of the tail in the left gluteal region. The catheters were filled with heparinized saline solution and flushed 3 times/wk. After surgery, the instrumentation leads were protected from mutilation by the dog with a jacket and/or protective collar. After a recovery period of 7-14 days the dogs were bred to unrestrained receptive females, and the pressure and EMG activity of the muscles were monitored.

The recording system consisted of a multichannel oscillographic recorder. The transducer (Ailtech, City of Industry, Calif.) for measuring CCP pressure via a catheter had a range of 0-250 psi (0-12,500 mmHg). The implantable subminiature pressure transducer (P-12, Konigsberg Instruments, Inc., Pasadena, Calif.) had a range of 0-300 psi (0-15,500 mmHg). All transducers used for measuring the CCP pressures were calibrated such that one needle would record pressures from 0 to 1,000 mmHg (100 mmHg/cm) and the other would record from 0 to 10,000 mmHg. (1,000 mmHg/cm) on the same recording paper. This was done by splitting signals into two amplifiers; thus during very high pressures the needle recording low pressures (0-1,000 mmHg) would be off the scale. Similarly, when the pressures were too low, both needles would record pressures. The low pressures (0-1,000 mmHg) at 100 mm/cm were calibrated with the aid of a specially built mercury manometer and the high pressures (0-10,000 mmHg or 0-200 psi) at 20 psi/cm (1 psi = 15.2 mmHg) were calibrated with a deadweight tester. The implantable transducer for measuring the bulbous glandis pressure was calibrated from 0 to 2,000 mmHg (100 mmHg/cm) with a special mercury manometer. The transducer for measuring the CSP pressure was calibrated from 0 to 1,000 mmHg (50 mmHg/cm).

The calibration of the transducers attached to catheters was checked before and after each breeding. The subminiature transducers were calibrated before implantation and recalibrated immediately after removal from the dog at the end of the experiment. The EMG activity of the external penile muscles was recorded via a two-channel telemetry system (Bio-Sentry Telemetry, Inc., Gardena, Calif.). All pressures were recorded via cables passing from the recorder to the dog.

After two to four control recordings were obtained from nine of the dogs in groups I and II, the IC muscles were anesthetized by local infiltration of 2% lidocaine 15 min prior to the breeding attempt to determine if the peak CCP pressure would be significantly reduced. One to three additional recordings of coitus were obtained at least 24 h after the lidocaine anesthesia to ascertain that the CCP pressure returned to preanesthetic level. The same sequence was used on three dogs in groups III and IV for the CSP and bulbous glandis pressure recordings, except the BS muscles were anesthetized with lidocaine instead of the IC muscles.

In order to determine the pressure required to rupture the CCP of the dog, 12 penile specimens were obtained and flushed with heparinized saline solution and packed in ice. The CCP of the specimens was ruptured on a system designed by Beckett et al. (6) to deliver 2,200 psi and was capable of withstanding pressures in excess of 3,000 psi.

Dunnett's test was applied to the pressure values to determine the significance of difference at 0.01 or 0.05 level (17).
RESULTS

Table 1 shows the CCP pressures associated with coitus recorded via needle-tipped polyvinyl catheter and transducer. The mean CCP pressure during predilation or the quiescent state of the penis was 26 mmHg. When a receptive female was brought into view, the CCP pressure rose to 161 mmHg at the initial stage of sexual excitement. The mean peak pressure during mount was 1,952 mmHg. The mean peak CCP pressure was the highest pressure that occurred during the period under study. During intromission, the mean peak CCP pressure was 5,296 mmHg. In dogs implanted with a subminiature transducer the absolute zero could not be checked because the entire transducer was within the CCP. However, when the penis was in a quiescent state, a relative zero was obtained, which was adequate for measuring the high peak CCP pressures. The mean peak CCP pressure during intromission was 7,434 mmHg, with a high and low of 15,735 and 2,275 mmHg, respectively.

The initial rise in the CCP and CSP pressures during coitus were 94 and 36 psi (663 and 236 mmHg), respectively. The mean peak CSP pressure during the initial stage of genital lock was 1,952 mmHg. In dogs implanted with a subminiature transducer the absolute zero could not be measured. The mean peak CSP pressure during the initial stage of genital lock was 4,006 mmHg. There was a gradual decrease in the CCP pressure after intromission until the end of the genital-lock phase. Once the penis was withdrawn from the vagina of the bitch, the mean CCP pressure approached the predilation stage.

During the mount and intromission phase of coitus, the EMG activity of the IC muscles was very intense and in phase with the CCP pressure peaks as shown in Fig. 2. In some dogs, the rhythmic contractions of the IC muscles continued for the entire phase of genital lock; in others, there was an intermittent pause. At the end of genital lock and for a period of 1 min or more, there was sporadic firing of the IC muscles. Anesthesia of the IC muscles with lidocaine reduced mean peak CCP pressures in dogs with catheters to 142 mmHg and in dogs with transducers to 204 mmHg during attempted coitus. The lowest and highest peak CCP pressures were 55 and 450 mmHg, respectively. Slight EMG activity of the IC muscles was evident in only one dog. None of the dogs were able to copulate, even though they mounted the bitch several times. The CCP pressures obtained 24 h or more after lidocaine anesthesia of the IC muscles were similar to the control breeding.

Table 1 shows the results with the needle-tipped polyvinyl catheter in the CSP. The mean CSP pressure during the quiescent state (predilation) of the penis for six dogs was 19 mmHg. The mean peak CSP pressures during dilution and mount were 97 and 123 mmHg, respectively. The mean peak CSP pressure during the intromission phase of coitus was 579 mmHg, with a high and low of 820 and 260 mmHg, respectively. During the initial stage of genital lock, the mean peak CSP pressure was 473 mmHg. Thereafter, there was a gradual decrease in CSP pressure during genital lock. The mean CSP pressure at 2 min after the end of genital lock was 23 mmHg, which was similar to the CSP pressure obtained during the predilation phase of coitus. The bulbus glandis pressures obtained by implanted transducers are also given in Table 1. The mean peak bulbus glandis pressure during dilation and mount was 128 and 416 mmHg, respectively. The mean peak bulbus glandis pressure during intromission was 1,280 mmHg.

The CSP pressure and the EMG activity of the IC and BS muscles in a dog during coitus are shown in Fig. 3. Usually the EMG activity of the BS muscles became evident shortly after the start of the EMG activity of the IC muscles. The EMG activity of the BS muscles was most intense during the intromission phase of coitus; then there were sporadic contractions of these muscles during the genital-lock phase that coincided with the pulsations of the CSP pressure. The highest CSP pressure was recorded during the intense activity of the BS muscles and not the IC muscles. Anesthesia of BS muscles with lidocaine reduced the peak CSP pressure to 800 mmHg and bulbuls glandis pressure to 230 mmHg. The CSP and bulbuls glandis pressures recorded 24 h after anesthesia of the BS muscles returned to its preanesthetic levels.

The pressure required to rupture the CCP was 1,656 psi (86,615 mmHg), with a low and high of 900 and 2,060 psi, respectively.

DISCUSSION

The initial rise in the CCP and CSP pressures during the mild state of erection and engorgement of the penis with blood was due to arterial vasodilation with increased flow of blood into the cavernous spaces (2, 5, 9, 14). During this initial phase of excitement there was no IC and BS muscle activity. As the dog became more excited sexually due to contact with female, the increase in the CCP pressure was significantly higher than arte-

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Values are means ± SE presented as mean of all observations pooled together. * CCP pressures recorded via polyvinyl catheter, n = 31. ** CCP pressures recorded via implantable pressure transducer, n = 26. * CSP pressures recorded via polyvinyl catheter, n = 11. ** Bulbus glandis pressures recorded via implantable pressure transducer, n = 11. Significantly different from predilation (poreinsent state of penis at 0.01 level. * Significantly different from distalation (mild erection of penis) at 0.05 level. ** Significantly different from intromission (mild erection of penis) at 0.05 level.
rial pressure. During this period, the dog usually mounted and dismounted the female repeatedly. With each successive mount there was an intense increase in the EMG activity of the IC muscles, but no appreciable activity in the BS muscles. During this stage the glans penis was usually protruded from the sheath and the CCP was erect. The CCP in the dog is attached to bone at both ends, the ischial tuberosity of the pelvis proximally and the os penis distally. Thus, when the CCP fills with blood under pressure the entire penis becomes rigid from the pelvis to the urethral process, which allows the male to achieve complete intromission during thrusting attempts. The highest increase in the CCP pressure occurs during intromission and was due to the contractile activity of IC muscles. This was substantiated by the fact that anesthesia of the IC muscles with lidocaine greatly reduced the peak CCP pressures and the dogs with low pressures were not able to copulate because of insufficient erection for intromission. Beckett et al. (5) reported that the CCP becomes a closed system during the period of high pressure, due to the contraction of the IC muscles that collapse the deep arteries and veins of the penis against the ischium. They also proposed that the tunica albuginea and fibrous trabeculae of the CCP form a fairly rigid structure and expand only slightly under pressure. When filled with a noncompressible fluid (blood), a small increase in volume would produce a large increase in pressure. If the CCP pressure increased to a level greater than that of the arterial pressure, the CCP would have to become a closed system, otherwise this pressure would be transmitted back into the circulatory system. With the kind of CCP pressures obtained in this study, it is proposed that the CCP system becomes a closed system in the dog similar to that reported for the goat, stallion, and bull.

The rise in CSP and bulbus glandis pressures above arterial blood pressure during coitus was mainly due to the contractile activity of the BS muscles. This was supported by the fact that the contraction of BS muscles was in phase with CSP pressure peaks and the anesthesia of BS muscles significantly reduced the CSP pressure. The CSP in the dog is not a closed system, but there seems to be a one-way flow system. The BS muscle compresses the urethral bulb and moves blood from the proximal end of the CSP to the distal end of the CSP and the bulbus glandis (11, 13).

In order for male and female to obtain genital lock, erection of the bulbus glandis is delayed until after there is complete intromission. Then the two are locked together because the constrictor vestibuli muscle of the female tightens behind the swollen bulbus glandis and because of mechanical retention of the penis in the vagina due to the enlarged bulbo glandis (8, 10). Hart et al. (11, 12) reported that the tonic contraction of the ischiourethral muscle partially occluded the venous return from the dorsal vein of the penis and probably aided the rapid filling of the bulbus glandis, after there was complete intromission. They also reported that sectioning of the ischiourethral muscle prevented the occurrence of genital lock, and they proposed that the detumescence of the bulbus glandis terminated the genital lock. Just prior to the end of genital lock, the activity of the BS muscles subsided and the pressure in the CSP and bulbus glandis decreased, which allowed the male to retract the penis and terminate genital lock. In these studies it was observed that engorgement of the bulbus glandis with a fully erect penis prior to intromission inhibited the dog from obtaining intromission, even though the dog mounted repeatedly and thrust the glans penis against the vaginal orifice.

The intense activity of the BS muscles indicated that the first phase of ejaculation in the dog occurred at the
end of intromission. The second phase of ejaculation probably occurred intermittently during genital lock. Hart et al. (11, 13) reported that the contraction pattern of the BS muscle during intromission and genital lock was consistent with the accepted concept that rhythmic contraction of this muscle aided in forceful expulsion of seminal fluid. From studies done with the goat (4), it was reported that the CSP pressure and BS muscle activity usually did not coincide with the CCP and IC muscle activity. This indicated that these muscles contracted alternately, which improved the movement of semen down the urethra. It was also proposed that the high CSP pressures would be transmitted across the urethral wall to enhance the movement of the semen down the urethra at the time of ejaculation.

The peak CCP pressures recorded by means of the needle-tipped polyvinyl catheter were lower than those recorded with subminiature transducers; however, there was overlap in the range of pressures recorded by the two methods. These differences were due to the elasticity of the polyvinyl catheter, dampening of the frequency response, and the spongelike nature of the CCP tissue, which limited the volume of the blood delivered to the catheter as described by Beckett et al. (2). The placement of the subminiature transducer within the CCP eliminated or greatly reduced the effects of volume displacement and of dampening. Therefore, the pressure measured with the implanted subminiature transducer would be closer to the physiological pressures.

The very high rupture pressures (86,614 mmHg) substantiated that the mean peak CCP pressure of 7,434 mmHg obtained during coitus was possible. The CCP in the dog has a fibrous membrane, the tunica albugina, that surrounds the corpus cavernosum penis. The thick tunica albugina and relatively dense intrinsic structure of the CCP forms a fairly rigid structure that can withstand very high pressures before rupturing.

![Diagram](http://ajplegacy.physiology.org/)
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REFERENCES