

# Innervation of the female internal genital organs: Whole-mount immunohistological observation in *Suncus murinus*

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## SUMMARY

The musk shrew, *Suncus murinus*, is a unique animal model for the study of female behavioral endocrinology, and by utilizing the physiological characteristics of ovulation during mating of *S. murinus*, key progress has been made in the study of the endocrine regulatory function of the ovary. The study of innervation of the ovary of *S. murinus* is particularly important. In the present study, the 3-dimensional structure of the neural innervation of the internal genital organs of *S. murinus* (n=11, female) was studied using whole-mount immunohistochemical staining with neurofilament protein antibodies. The innervation of the ovary in *S. murinus* contains the superior ovarian nerve, which runs along the suspensory ligament of the ovary, and the ovarian plexus nerve, which runs along the ovarian artery and vein. The innervation of the uterus originates from the lower hypogastric plexus running in the pelvic peritoneum and along the uterine artery and vein. There was abundant communication between the ovarian plexus nerve and the lower hypogastric plexus of the pelvic peritoneum. The present study is the first to visualize the (NFP-positive) innervation of

the female internal genital organs of the experimental animal *S. murinus* by the whole-mount immunohistochemistry method. The abundant communication between the ovarian plexus nerve and the lower hypogastric plexus of the pelvic peritoneum provides an additional pathway for the neural regulation of the ovary.

**Key words:** Superior ovarian nerve – Ovarian plexus nerve – Ovarian suspensory ligament – Lower hypogastric plexus – *Suncus murinus*

## INTRODUCTION

Insectivora are the third-largest mammalian order, comprising a number of unusual species considered to be the most primitive of modern eutherian mammals. The musk shrew, *Suncus murinus* (*S. murinus*), is a convenient and practical laboratory animal (Temple, 2004). *S. murinus*, is a unique animal model for the study of female behavioral endocrinology (Rissman, 1990), and has proven to be a useful model for elucidating the peripheral cues and neuronal mechanisms that underlie nutritional infertility (Temple, 2004). Most current and past research on this species has focused on

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the endocrinology of female musk shrews. Unlike conventional small mammal models, female musk shrews have no spontaneous ovarian cycle. The ovaries of adult unmated females do not undergo spontaneous follicular development. At the time of mating, only small relatively immature follicles are present. Consequently, ovarian hormone production is not cyclic (Fortune et al., 1992; Matsuzaki et al., 1997a; Matsuzaki et al., 1997b).

Utilizing the physiological characteristics of ovulation during mating in *S. murinus*, key progress has been made in the study of the endocrine regulatory function of the ovary (Inoue et al., 2011; Inoue et al., 2022). In recent years, it has been established that ovarian functions are not solely regulated by hypophyseal hormones, with neural influences also playing a critical role (Dogany et al., 2010). In addition, the ovarian nerves are involved in various pathological conditions in the ovary. An accurate understanding of ovarian innervation is important when performing surgery (Pastelin et al., 2023), so the study of the innervation of the ovary of *S. murinus* is of particular import.

Studies of female internal genitalia innervation to date have mainly reported on the oviduct in pigs (Czaja et al., 2001), ovaries of rats and guinea pigs (Burden, 1972), ovaries in rats (Payer, 1978; Baljet et al., 1979; Lawrence and Burden, 1980; Pastelín et al., 2017; Bravo-Benitez et al., 2022; Pastelin et al., 2023); sympathetic denervation of the rat ovary (Gibson et al., 1984; Luna et al., 2003); and physiological studies of the superior ovarian nerve (Rosas et al., 2018; Ramírez Hernández et al., 2020). However, the research methods involving these species are mainly limited to formaldehyde-induced fluorescence and acetylcholinesterase (Baljet and Drukker, 1979) and the fluorescent retrograde tracer True blue (Klein and Burden, 1988), adrenergic cholinergic, and presumably sensory innervation in porcine fetuses (Franke-Radowiecka et al., 2019). Three-dimensional visualization of nerves is greatly limited.

As an experimental animal, *S. murinus* has been shown to exhibit general morphological characteristics, especially in the visceral system, which is more similar to that of humans than other cur-

rently used laboratory animals, such as mice, rats, and rabbits (Oda S and Kondo K, 1977; Tsutsui et al., 2009). This study suggests that this animal is also more valuable than general laboratory animals in terms of intrahepatic nerve distribution. In our previous studies, *S. murinus* has been employed for clinico-anatomical and morphological studies of the innervations of the pancreas (Ren et al., 2016), extrahepatic biliary tract (Ren et al., 2017), intrahepatic (Ren et al., 2025a), and hepatic vein and its sphincter (Ren et al., 2025b) via comparative studies on humans.

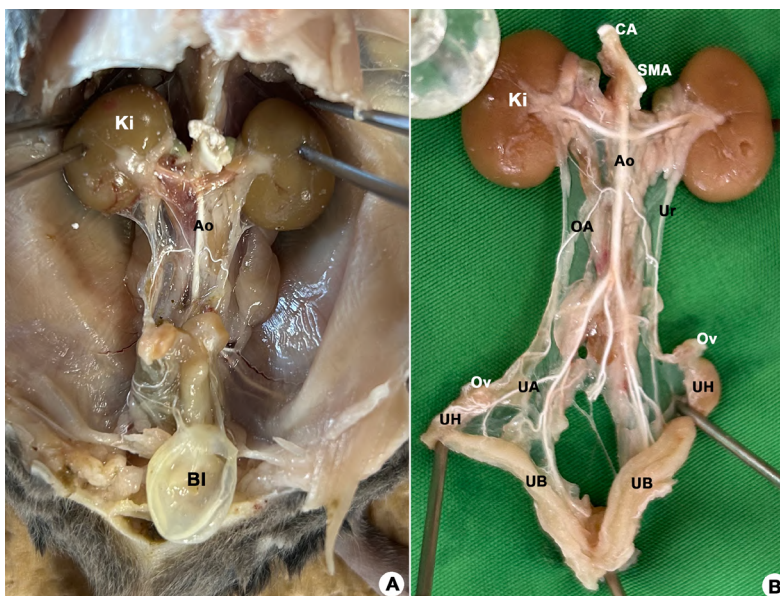
Based on our recent study resolving the three-dimensional structure of the distribution of nerves supplying of the testis, epididymis, and accessory sex glands of *S. murinus* (Dai et al., 2019), the present study used whole-tissue immunohistochemical staining with neurofilament antibodies to examine the extrinsic innervation of the ovaries and uterus in *S. murinus*.

## MATERIALS AND METHODS

### Animals

Experiments were performed using adult female *S. murinus* (n = 11, weighing 65-90 g, aged 4-6 months) from an outbred KAT strain established from a wild population in Kathmandu, Nepal (Oda et al., 1992). The specimens were obtained from a closed breeding colony, and they were bred and maintained in our laboratory at the Functional Morphology Laboratory, Department of Frontier Health Sciences (Tokyo Metropolitan University, Tokyo, Japan). A sample size of 11 adult female *S. murinus* was considered appropriate for this descriptive anatomical study. Given the expected low inter-individual variability in the innervation patterns of this species, and considering that previous similar studies of ovarian and reproductive tract innervation have used comparable sample sizes (e.g., Pastelin et al., 2023, n=10 rats; Dai et al., 2019, n=9 *S. murinus*), this number was deemed sufficient to reliably characterize the neural distribution in the female internal genital organs.

Adult *S. murinus* specimens were kept individually after weaning (28 days after birth) in plastic cages equipped with a wooden nest box contain-



**Fig. 1.-** A) Overall image of the specimen before whole-mount immunohistochemistry staining. To visualize the entirety of the ovary and uterus, the uterine body was divided mid-sagittally into right and left sections (B). Ao, abdominal aorta; Bl, bladder; CA, celiac artery; Ki, kidney; OA, ovarian artery; Ov, ovary; SMA, superior mesenteric artery; UA, uterine artery; UB, uterine body; UH, uterine horn; Ur, ureter.

ing paper strips, and maintained in a conventionally conditioned animal room: 23 to 27 °C, no humidity control, and a 12-h day/light cycle. Commercial trout pellets and water were provided ad libitum.

All experimental procedures were approved by the Tokyo Metropolitan University Institutional Animal Care and Use Committee (no. A3-23, A4-20, A5-15, A6-15). Animals were housed and handled in accordance with the Guide for the Care and Use of Laboratory Animals and the Guide for the Care and Use of Experimental Animals of the Canadian Council on Animal Care.

### Tissue preparation

Female *S. murinus* were first anesthetized with ether and then administered an intraperitoneal injection of somnopenyl (pentobarbital sodium, 0.6 ml/kg bodyweight). After complete anesthesia and euthanasia of the animals, the chest cavity was opened, and a catheter was inserted into the left ventricle while the right atrium was incised. Afterwards, perfusion with phosphate-buffered saline (PBS; 0.01 M, pH 7.4) and 4% paraformaldehyde (PFA) was performed. After perfusion, white neoprene latex was injected to label the blood vessels. Next, the intraperitoneal cavity was immersed overnight in 4% PFA, and the internal

urogenital organs, including the kidneys, lower abdomen/pelvis, and blood vessels along the posterior abdominal wall were removed (Fig. 1A). The bladder was separated from its neck, the body of the uterus was sectioned along the midline, and the complete specimen was subjected to whole-mount immunostaining (Fig. 1B).

### Experimental protocols: whole-mount immunohistochemistry

Whole-mount immunostaining of *S. murinus* was performed as previously described (Ren et al., 2016, 2017, and 2025a). In brief, after the fixed specimen was washed with PBS and rocked gently on the nutator for 4 h, it was treated with 1% (w/v) orthoperiodic acid for 20 min at room temperature (RT) to prevent any intrinsic peroxidase reaction. It was then incubated in freshly prepared 0.004% (w/v) papain in 0.025 mol/L Tris-HCl buffer (pH 7.6) at 37 °C for 2 h in a constant-temperature bath with gentle rocking. The specimens were washed with PBS for 50-60 min at RT and then stored in 4% PFA at 4 °C overnight. The next day, the stored specimens were washed with PBS 4 times for 1 h each at RT, as described above. The specimen was then immersed in 2.5% (w/v), 5% (w/v), and 10% (w/v) sucrose for 30 min each, followed by freezing at -20 °C for 30-60 min and thawing at RT, until completely thawed; this

cycle was repeated three times. The specimens were then stored overnight in 2% Triton X-100 at 4 °C overnight. The next day, the specimen was incubated with the primary antibody in PBS containing 0.2% bovine serum albumin, 0.3% Triton X-100, and 0.1% sodium azide for 3 days at 4 °C and continuously rocked gently on the nutator. After thorough washing in PBS, the specimens were incubated with the secondary antibody in a dilution buffer containing 0.2% bovine serum albumin (BSA) and 0.3% Triton X-100 for 3 days at 4 °C. After thorough washing in PBS, coloration was performed in 0.05 mol/L Tris-HCl buffer containing 0.002% 3,3'-diaminobenzidine (DAB) and 0.1 ml/L H<sub>2</sub>O<sub>2</sub> overnight at 4 °C. Stained preparations were stored in glycerin to ensure transparency.

The control experiments consisted of the following: (1) omission of the primary antiserum and (2) substitution of the primary antibody with PBS containing 0.2% bovine serum albumin, 0.3% Triton X-100, and 0.1% sodium azide. These controls were performed on the sections at the same time as the primary antibody treatment. The control data are not shown.

After the above-described staining was completed, the specimens were floated in PBS, and a stereomicroscope (objective lens can magnify 0.8 to 8 times; Nikon, Tokyo, Japan) was used to observe and analyze the intrahepatic and extrahepatic nerve distribution, and took photograph.

The primary antibodies used were an anti-neurofilament protein (NFP) antibody (diluted 1:600), a monoclonal mouse anti-all neurofilament consisting of three subunit proteins: NF-H (200 kDa), NF-M (160 kDa), and NF-L (70 kDa) (M0762, lot 089, clone: 2F11; Dako). The dilution solution of the primary antibody was 0.2% (w/v) BSA and 0.3% (v/v) Triton X-100 with 0.01 M PBS (pH 7.4). The secondary antibody labeled with peroxidase-conjugated affinity-purified sheep anti-mouse IgG (HRP, MBL code 330) was diluted to 1:600 with 0.2% (w/v) BSA, 0.3% (v/v) Triton X-100, and 0.1% (w/v) sodium azide with 0.01 M PBS (pH 7.4).

## RESULTS

The innervation of the ovary in *S. murinus* indi-

cated that the superior ovarian nerve (SON) ran along the suspensory ligament of the ovary (Fig. 2), and the ovarian plexus nerve (OPN) ran along the ovarian artery and vein (Figs. 3A and 4).

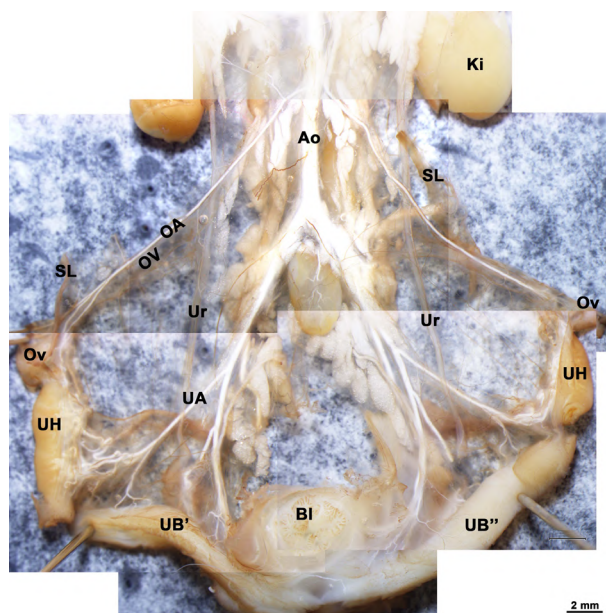
The OPN originated from the celiac-superior mesenteric plexus (Fig. 2). The nerves along the ovarian suspensory ligament originate from the suprarenal plexus (data not shown). No left-right differences in ovarian nerve distribution were found in *S. murinus*.

The innervation of the uterus originates from the lower hypogastric plexus running in the pelvic peritoneum (Figs. 4 and 5) and along the uterine artery and vein. The OPN running along the ovarian arteries and veins also extended along the branches of the blood vessels to the uterine horns and innervated the latter (Figs. 3, 4, and 5B). There was abundant communication between the OPN running from the ovarian artery and vein and the lower hypogastric plexus of the pelvic peritoneum. (Fig. 4).

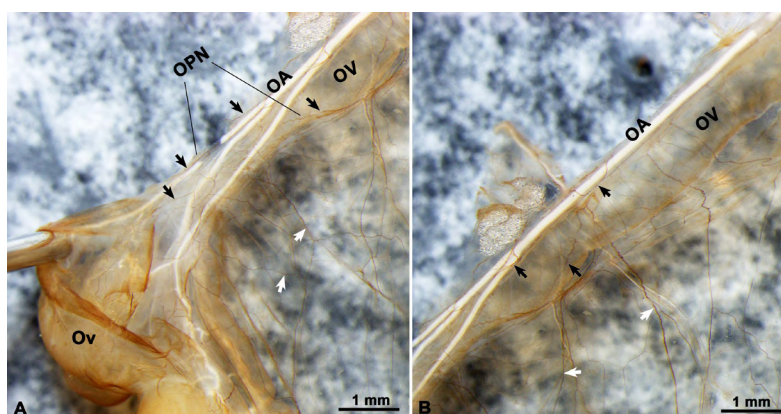
## DISCUSSION

In the present study, we used the whole-mount immunohistochemistry method to visualize the innervation of the female internal genital organs of the experimental animal *S. murinus*. The innervation of the ovary in *S. murinus* contained the SON, which runs along the suspensory ligament of the ovary, and the OPN, which runs along the ovarian artery and vein. The innervation of the uterus originates from the lower hypogastric plexus running in the pelvic peritoneum and along the uterine artery and vein. There was abundant communication between the OPN running from the ovarian artery and vein, and the lower hypogastric plexus of the pelvic peritoneum. The existence of these communicating branches provides an additional pathway for the neural regulation of the ovary.

In rats, autonomic nerves arrive at the ovary via two pathways: the SON in the suspensory ligament; and the OPN, which runs jointly to the ovarian artery and vein (Lawrence and Burden, 1980; Pastelín et al., 2017). The ovarian nerves in rats are derived from the celiac plexus, intermesenteric plexus, and upper lumbar splanchnic nerves.



**Fig. 2.-** The anatomical location of the ovary (Ov) and uterus in *Suncus* by whole-mount immunocytochemistry staining with NFP antibody. To visualize the ovary, the uterine body was divided mid-sagittally into right and left sections (UB' and UB'', respectively) and unfolded. Ao, aorta; Bl, cross-section of neck-cut bladder; Ki, kidney; OA, ovarian artery; OV, ovarian vein; SL, suspensory ligament; UA, uterine artery; UB, uterine body; UH, uterine horn; Ur, ureter.



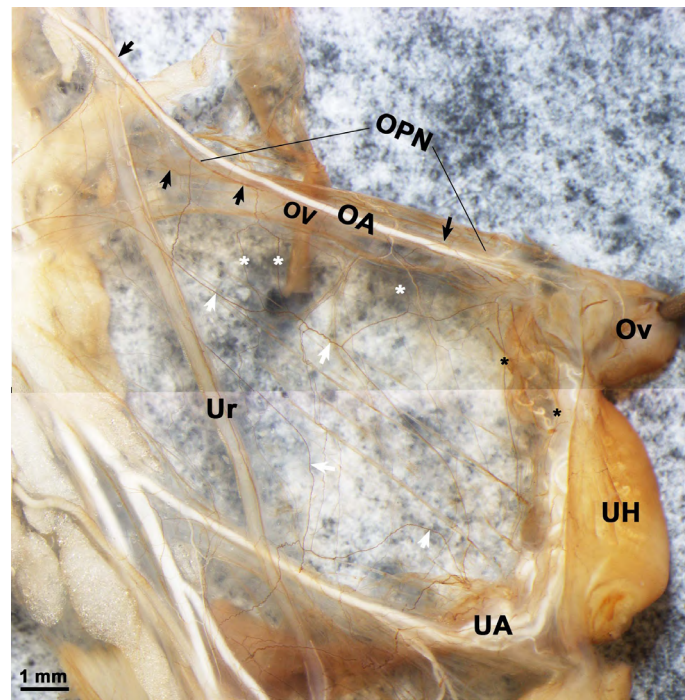
**Fig. 3.-** Innervation of the right ovary (Ov). Black arrows indicate the ovarian plexus nerve (OPN) running along the ovarian artery (OA) and vein (OV). White arrows indicate the communicating branches between the OPN and the nerves of the uterus, which run in the peritoneum originating from the OPN.

Bundles of nerve fibers run from the suprarenal ganglion in the celiac plexus in the direction of the suspensory ligament of the ovary (Baljet and Drukker, 1979; Pastelin et al., 2023). These results are consistent with our findings for *S. murinus*.

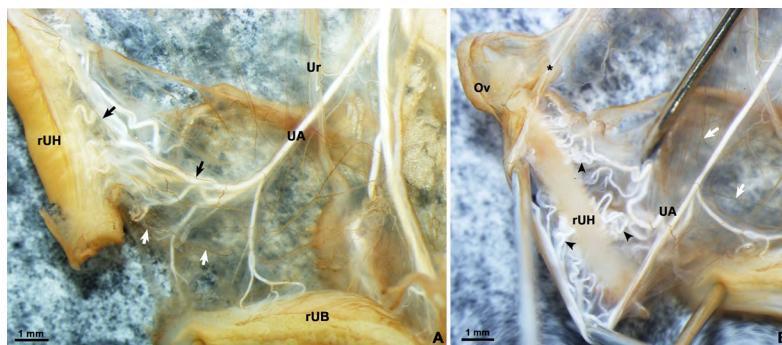
In rats, the ovarian suspensory ligament is a fibromuscular, cord-like structure that extends cranially from the hilum of the ovary to the lower edge of the thoracic cage. Blood vessels and innervation run along the suspensory ligament wall (Pastelin et al., 2023). SON is one of the main routes innervating the ovary in *S. murinus*, and the origin and pathway of SON are consistent with

those in rats. Regarding the relationship between OPN and uterine innervation in *S. murinus*, our results agree with those described by other authors, the OPN innervates the ovary, bursa, oviduct (Payer, 1978), and cranial uterine horns in rats (Lawrence and Burden, 1980).

Morales et al. (1998) pointed out the effect of unilateral or bilateral SON sections on the ovulatory response to gonadotropin administration in prepubertal rats, because the ovaries are innervated via the SON, ovarian plexus, and vagus nerve. The results obtained in unilateral denervated animals suggest that the ovaries regulate the effects of go-



**Fig. 4.-** Innervation of the left ovary (Ov) and uterus. Black arrows indicate the ovarian plexus nerve (OPN) running along the ovarian artery (OA) and vein (OV) and innervating the ovary. White arrows indicate nerves running in the peritoneum and innervating the uterus. White asterisks indicate the communicating branches between the two above. Black asterisks indicate the nerves innervating the uterine horn (UH) originating from the OPN. Ur, ureter.



**Fig. 5.-** Innervation of the uterus. Black and white arrows indicate nerves along the uterine arteries (UAs) and peritoneum to the uterus, respectively. Ov, ovary; rUB, right uterine corpus after midline incision. Black arrowheads indicate the abundant branches of the uterine artery to the uterine horn (rUH). The asterisk indicates the artery supplying the uterine horn branching from the uterine artery.

nadotropins in a stimulatory manner through the innervation of the SON, leading to ovulation. Hormonal treatment of rats with bilateral SON removal induced ovulation, indicating that the effects of bilateral SON removal on ovulation are not the sum of the effects of left and right denervation, which means that gonadotropins have a modulatory effect on ovulation through other neural pathways.

Furthermore, Selstam et al. (1985) reported that adrenergic nerves reach the ovary via two routes: along the ovarian artery, and via the suspensory ligament. Denervation of nerves along the arter-

ies does not affect the ovulatory process. Those authors' study showed that denervation caused by transection of the ovarian suspensory ligament does not affect the ovulatory process, and adrenergic nerves in the suspensory ligament do not seem to be necessary for ovulation. It seems unlikely that adrenergic nerves reach the corpus luteum via the suspensory ligament, as transection of this structure did not alter the norepinephrine content in the corpus luteum.

Our present findings show abundant communication between the OPN running from the ovarian artery and vein and the lower hypogastric

plexus of the pelvic peritoneum. Therefore, we cannot exclude the existence of a third route for adrenergic nerves to reach the ovary; that is, the abundant communication between the OPN and lower hypogastric plexus may compensate for the denervation effect that may occur after resection of the suspensory ligaments.

## CONCLUSION

The present study is the first to visualize the (NFP-positive) innervation of the female internal genital organs of the experimental animal *S. murinus* by the whole-mount immunohistochemistry method. It should be noted that *S. murinus* is a unique animal model for the study of female behavioral endocrinology (Rissman, 1990), and has proven to be a useful model for elucidating the peripheral cues and neuronal mechanisms that underlie nutritional infertility (Temple, 2004). We noted abundant communication between the OPN running from the ovarian artery and vein and the lower hypogastric plexus of the pelvic peritoneum in *S. murinus*. The existence of this communicating branch provides an additional pathway for the neural regulation of the ovary.

## AUTHORS' CONTRIBUTIONS

SY designed and conceived the study. KR, XC, and TY participated in experiments. KR, XC, and SY analyzed the data. KR and XC wrote the manuscript. SY revised the manuscript. All authors have contributed to the final version of this manuscript. All authors have read and approved the final manuscript.

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