

## FEATURE ARTICLE

# The *Hermunculus*: What Is Known about the Representation of the Female Body in the Brain?

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**The representation of the body in the brain, the homunculus, was posited by Wilder Penfield based on his studies of patients with intractable epilepsy. While he mapped both male and female patients, Penfield reports little about the females. The now iconic illustration of the map is clearly male with testicles, penis, and no breasts. In order to bring attention to this omission and to stimulate studies of female somatosensory cortex (SS), we discuss what is known about the map of the female body in the brain, including Penfield's findings in his female patients and subsequent work by others exploring the human female SS. We reveal that there is much we do not know about how the entire female body is represented in the brain or how it might change with different reproductive life stages, hormones, and experiences. Understanding what is and is not currently known about the female SS is a first step toward fully understanding neurological and physiological sex differences, as well as producing better-informed treatments for pain conditions related to mastectomy, hysterectomy, vulvodynia, and fibromyalgia. We suggest that the time is ripe for a full mapping of the female brain with the production of a hermunculus.**

**Keywords:** genitalia, homunculus, sex differences, somatosensory cortex, steroid hormones

### Penfield's Homunculus

Wilder Penfield, credited with establishing the “map” of the human body in the sensory and motor cortices, was principally interested in demonstrating localization of function within the human brain (Penfield and Rasmussen 1950). Although descriptions of somatic sensory areas within the cortex appear in Penfield's work as early as 1930 (Penfield 1930), it is his work with Boldrey featured in “Brain” (Penfield and Boldrey 1937) that begins to describe the representation of different body regions in the brain and presents the first pictorial somatosensory map, or sensory “homunculus” (Schott 1993). In his later work with Rasmussen (Penfield and Rasmussen 1950), he fully describes what he has learned over a career of brain surgery on epileptic patients, who were asked to describe sensory perception in response to direct cortical stimulation by electrodes. Medical artist Hortense Cantlie illustrated these data, showing the projection of body areas sensed and reported during Penfield's passage of electrical current (Griggs 1988). Cantlie's interpretation, depicting a human body arranged along the edge of a cross section through the precentral and postcentral gyri, the size of each part corresponding to the extent of its cortical representation, has become iconic and is still widely reproduced.

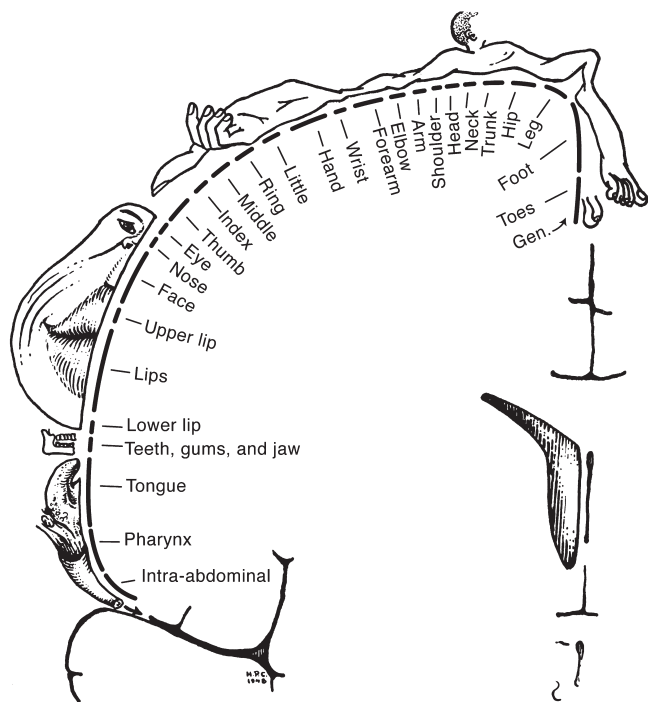
### The Omission of Female Anatomy

A quick glance at this homunculus, or “little man,” in the brain reveals that it has a penis and testicles, but no breasts, vagina, clitoris, uterus, or ovaries (Fig. 1). Based largely on early direct cortical stimulation studies on epileptic patients and merging Penfield's findings in primary and secondary somatosensory cortex (S1 and S2), this map of the human body in the brain omits uniquely female anatomy. Furthermore, it does not convey what we now understand about brain plasticity in response to experience and to hormones.

Why women were so little discussed in Penfield's papers and not represented in Cantlie's original illustration is an open question. Over the course of Penfield's career, he studied a total of 1065 patients, 107 of whom were women and 121 for whom sex was not reported (these figures are estimates, as some of Penfield's works are reviews of his own previous publications and individual patients may be included in multiple analyses). In his book with Rasmussen, Penfield reports on a total of 400 operations of which at least 9 were performed on women (one subject's sex was not indicated; Penfield and Rasmussen 1950). The rest of his publications have scant reports on women specifically. Thus, he may simply not have had enough data to discriminate responses of women from those of men. As well, his data may have been muddled by not ascertaining where in the menstrual cycle his female patients were, or if they were past the age of menarche. It is also quite possible that historical issues of propriety influenced the reports of sensations by the women being studied, Penfield's reports of what they said, and the illustrator's comfort with drawing the genitals of women.

### Somatosensory Representations of Male and Female May Differ

There are good reasons to suspect that female and male somatosensory representations differ. While the map would contain embryologically homologous body regions such as the glans penis/clitoris, scrotum/labia, and testicles/ovaries, female organs might be represented with a different somatotopy, size, or variability of representation at different stages of the menstrual cycle, during pregnancy, or with respect to other body regions that are more or less sensitive in males and females. Even when the structures are embryologically homologous, anatomically the locations of some of these organs differ—for example, most of the clitoris, the homologous structure to the penis, is internal (O'Connell et al. 2005)—and more recent mapping has revealed that the viscera activate brain regions distinct from those activated by external body structures (Kern et al. 2001). For these reasons and more, it is not sufficient to assume that the male and female



**Figure 1.** Penfield's sensory homunculus. Cortical representations for various body parts as mapped onto the pre- and postcentral gyri in the parietal cortex of humans. Note the sensory localization for the genitals, depicted by a penis, located deep within the medial wall. There is no sensory representation for the female labia and/or breasts. Modified from Penfield and Rasmussen (1950).

somatotopic maps are the same and that, therefore, the male can stand as the universal representation. Furthermore, some recent studies suggest that even the present model of the human male somatosensory cortex (SS) may not be organized in the order that Penfield proposed (Kell et al. 2005).

The purpose of the present paper is to explore what is known about the representation of the human female body in the brain. To do this, we discuss all available human studies that document what is and is not currently known about this topic as well as relevant animal studies. (We searched the following databases for English-language literature that examined the female SS: PubMed, MedLine/Ovid, Google Scholar, CRISP/RePORTER, and Scholars Portal (PsycINFO). Key words used singly and crossed were: female, sex, sex differences, SS (primary and secondary), homunculus, brain mapping, breast, clitoris, vagina, cervix, menstrual cycle, genitalia, "Wilder Penfield," and plasticity (search conducted on 8 July 2010). This produced a total of 604 citations. From these, we excluded all that dealt with male humans or nonhuman animals exclusively and were left with 52 citations that dealt with the somatotopic representation of the female body and female-specific cortical organization and plasticity, all of which are included in the present review.) Recent research proposes somatotopic localizations for the human female genitals and breasts, as well as brain areas involved in female orgasm (Table 1). Taken together, these represent the beginning of a female somatotopic map—or "hermunculus"—that would take into account both sexually differentiated body surface and internal organs as well as the plasticity that may well occur during different reproductive life stages, including pregnancy, menopause, and the ovarian cycle.

## The Human Female SS: What Is Known

### Direct Brain Stimulation

Penfield used direct brain stimulation of patients with epilepsy in order to identify regions around the epileptic focus. Prior to these experiments, however, Grünbaum and Sherrington demonstrated that in nonhuman primates there is an anal and vaginal motor region located on the dorsal surface of the precentral gyrus (primary motor cortex, M1; Grünbaum and Sherrington 1901). Penfield and Boldrey tried to show that this was the case for the human female as well and also hypothesized that the genitalia and rectum (both male and female) would be represented within the longitudinal fissure, posterior to the feet. Unfortunately, Penfield and Boldrey never include these in their somatotopic map and attribute this omission to insufficient evidence to support a rectal and genital localization (Penfield and Boldrey 1937). Penfield and Rasmussen proceeded to localize the labium and breast, but not anus or rectum, to the right postcentral gyrus in a single case—patient E.C., a 27-year-old woman who had a tumor removed from the right postcentral gyrus. Prior to the excision, E.C. experienced spontaneous sensory seizures that involved her left labium and left breast. E.C.'s genital sensations were described as a tingling that shifted between her left buttock, labia, and breast (including the nipple). On one occasion, cortical stimulation of the posterior postcentral gyrus produced sensation in the left buttock and twitching of the left foot (Penfield and Rasmussen 1950).

E.C. is the only female patient of 107 identified in Penfield's works to report genital sensation following stimulation of the cortex. Penfield and Rasmussen state that reports of sensation in the lower sacral and genital regions were rare and that their experiments never elicited any type of "erotic sensations" in any of their test patients (Penfield and Rasmussen 1950, Penfield and Kristiansen 1951). Thus, it seems that this one case was the basis for Penfield and Rasmussen's suggestion that the external female genitalia and breast are localized on the medial wall of the cerebral hemisphere posterior to the motor representation of the foot in the precentral gyrus motor area; E.C. is referred to multiple times to support this assertion (Penfield and Boldrey 1937; Penfield and Rasmussen 1950; Penfield and Kristiansen 1951; Penfield and Jasper 1954).

### An Early Case Study

Along with Penfield's work, one of the earliest case studies to consider the relative locations of various elements of female genitalia was that of a woman with epilepsy (Erickson 1945). This patient was diagnosed with "erotomania" because she experienced vaginal sensations similar to those felt during intercourse in tandem with her seizures. Based on the Jacksonian progression of these sensations, Erickson inferred a close relationship among the contralateral sensory areas for the vagina, leg, abdomen, toe, arm, and ocular motor regions. Although he offers no sequential order for the cortical representation of these sensory and motor areas, he does suggest that the suspected causal tumor in the patient's right parietal parasagittal region (deep within the cerebral hemisphere) put pressure on a proposed genital region within the medial SS. In support of this hypothesis, Erickson notes a relief from the "nymphomaniac" symptoms upon removal of the tumor, as reported during a 1-year follow-up (Erickson 1945). This report came before Penfield reported on E.C. explicitly but supports his mapping of the relationship of the foot to the female genitalia.

**Table 1**

List of studies localizing somatotopy of human female anatomy

Author	Year	n	M/F	Condition	Methods	Somatotopy
Allison et al.	1996	18	F	Epilepsy	SSEP: electrodes either side of clitoris (pudendal n.)	Clitoris on medial wall of SS in paracentral lobule, anterior to foot
Aurbach et al.	2009	1	F	Premastectomy	fMRI	Breast lateral to longitudinal fissure
Erickson	1945	1	F	Tumor-related seizures	Case study	Genital region proposed within medial SS
Georgiadis et al.	2006	12	F	Healthy	PET	Clitoris: dorsal surface of postcentral gyrus in S1; laterally, left postcentral gyrus in S2. During orgasm, also clusters in M1, paracentral lobule, dorsal aspect of central sulcus
Kell et al.	2005	8	M	Healthy	fMRI	Toe, lower abdomen, penis (medial to lateral—not on medial wall)
Kern et al.	2001	28 M, 15 F	F and M	Healthy	PET (rCBF)	Rectum: sensory and parietooccipital cortex in M and F; anterior cingulate gyrus in F only
Komisaruk et al.	2011	11	F	Healthy	fMRI	Clitoris, vagina, cervix: medial wall, paracentral lobule, deep within cortex, inferior to toe; Nipple: same location as genitals; also represented in cortical area devoted to trunk
Michels et al.	2010	15	F	Healthy	fMRI: electrodes either side of clitoris (dorsal clitoral n.—branch of pudendal n.)	Clitoris: distal S1 lateral to toe; parietal operculum (S); other non-SS regions
Penfield and Rasmussen	1950	1	F	Epilepsy	Direct brain stimulation	Labia, buttock, breast: medial wall posterior to motor representation of foot
Pukall et al.	2005	28	F	Vulvar vestibulitis (14) and controls (14)	fMRI	Vagina in S2
Rothmund et al.	2005	13	F	Healthy	SSEPs	Nipple: lateral to longitudinal fissure between groin (medial) and finger (lateral)
Yang and Kromm	2004	77	F	Healthy	SSEPs: electrodes on clitoral hood and sides of clitoris and in vaginal introitus (perineal and dorsal n.s)	External genitals: medial wall

Note: studies listed by author in alphabetical order. n, subject number; M, male; F, female; n., nerve.

### Somatosensory Evoked Potentials

Subsequent studies used a combination of body stimulation and cortical surface recordings to identify the body regions on the medial wall of SS. To localize the clitoris, Allison and colleagues stimulated the dorsal pudendal nerve in 18 women with epilepsy (mean age not provided). Electrodes were placed on either side of the clitoris and cortical response was recorded from a point just anterior to Penfield's representation of the foot, on the medial surface of SS. In agreement with Penfield, these authors report that representation of the female genitals, and specifically the clitoris and perineum, is within the medial wall of SS, anterior to the representation of the foot in the paracentral lobule (Allison et al. 1996, Table 1).

Kim and colleagues used evoked potentials to investigate possible changes in the innervation of the upper vagina pre- and posthysterectomy. Since the same nerve and branches innervate the upper vagina, uterus, and bladder, the concern might be that the branches of this nerve innervating some structures might be damaged in surgery. Twenty patients (mean age = 44 years) had either removal of the uterus only or removal of the uterus plus one or both fallopian tubes and ovaries. A stimulating electrode was applied to both right and left sides of the upper one-third of the vaginal wall on the day of admission prior to surgery (baseline) and 3 months postoperatively. With respect to the vaginal innervation, no significant differences were detected between the pre- and postoperative latencies or amplitudes, suggesting that the sensory pathway of the upper vagina, which is mediated by the pelvic nerve and specifically the uterovaginal plexus of Frankenhäuser, is not affected or that cortical plasticity led to very rapid recovery of any changes to this pathway (Kim et al. 2001).

Yang and Kromm expanded upon Allison's study by studying cortically evoked potentials in response to stimulation of the perineal and dorsal nerves which, like the pudendal, are all branches of the pelvic nerve that innervates the clitoris and vagina. To stimulate the dorsal nerve, 77 female participants

(mean age = 29.3 years) had self-adhesive electrodes attached to the central portion of their clitoral hoods as well as to either side of the clitoris. To stimulate the perineal nerve, a probe with 2 electrodes spaced 1 cm apart was inserted into the vagina and attached to either labia minora. Both left and right sides of the vagina were tested in all subjects. Electrodes placed on the scalp near the medial wall detected significant SSEPs from dorsal and perineal nerve stimulation (Yang and Kromm 2004). These findings also concur with Penfield and Rasmussen's localization (Penfield and Rasmussen 1950). There remains the open question of whether the internal portion of the clitoris is represented in the same cortical region as the external portion since the probe only stimulated 1 cm into the introitus.

Rothmund localized the representation of the female trunk and breast by measuring evoked potentials after stimulation of the nipple, groin, and first digit. The stimulus was applied via ring electrodes on both sides of the body in 13 healthy women (mean age = 25 years). Evoked potentials for nipple stimulation were recorded lateral to the longitudinal fissure localized between the representation of the groin medially and of the first digit laterally, roughly matching Penfield and Rasmussen's somatotopic placement of the male trunk (Rothmund et al. 2005).

### Functional Imaging

Georgiadis and colleagues used positron emission tomography (PET) to localize cortical activity in the female brain during clitoral stimulation and orgasm. Since clitoral stimulation was part of the experimental design, it is possible to infer a location for clitoral representation within the homunculus from the results of this study. PET measures regional cerebral blood flow (rCBF) as it relates to experimental conditions, such as stimulation and rest, and allows inference about the function of brain regions associated with peaks in rCBF. Twelve healthy women (mean age = 34 years) were evaluated during a nonsexual resting state, clitoral stimulation, and orgasm. As a control for motor output, a condition of imitation orgasm—which consisted

of voluntary, rhythmic, repetitive contractions of the hip, buttock, pelvic floor, and abdominal muscles during stimulation of the clitoris—was also analyzed. Stimulation of the clitoris showed significant rCBF activation bilaterally on the dorsal surface of the postcentral gyrus in S1 and laterally in the left postcentral gyrus within S2, or parietal operculum. Brain activity during orgasm showed peak rCBF in S1 with significant clusters of activity in dorsal M1 cortex, the paracentral lobule, and the dorsal aspect of the central sulcus (Georgiadis et al. 2006).

From this, we can infer that the clitoral localizations suggested by this study are not consistent with Penfield's localization of the homologous structure, the penis, on the medial wall (or paracentral lobule) of the postcentral gyrus, nor with traditionally postulated localizations (Grünbaum and Sherrington 1901; Erickson 1945), and in nonhuman primate studies (Woolsey et al. 1942). However, they are consistent with results from Woolsey's later studies on nonhuman primates (Woolsey et al. 1979) and more recent studies that utilize functional magnetic resonance imaging (fMRI) to reexamine the somatotopic representation of the human male penis, which has also been localized to the dorsal surface of the postcentral gyrus, lateral to the representation of the toe and not, as mapped by Penfield, on the paracentral lobule (Kell et al. 2005).

Komisaruk and colleagues used fMRI to map the clitoris, vagina, and cervix during tactile self-stimulation and orgasm in healthy women (Komisaruk et al. 2011) and have also investigated cortical activation during self-stimulation-induced orgasm in women with complete spinal cord injury (Komisaruk et al. 2004; Komisaruk and Whipple 2005). The most recent of these studies is the first to provide a female-specific sensory map of the genitalia—which includes the clitoris, cervix, and vagina—on the homunculus. The authors found clustered but differentiated genital representations in 11 subjects (ages 23–56, mean age not provided), following stimulation of the nerves that directly innervate the clitoris (pudendal nerve), vagina (pelvic nerve), and cervix (pelvic, hypogastric, and vagus nerves) (Komisaruk et al. 2011). In a superior-to-inferior sequence, the clitoris, cervix, and vagina activated regions of the paracentral lobule, consistent with Penfield and Rasmussen's placement of the genitals deep within the cortex and inferior to the representation of the toe (Penfield and Rasmussen 1950). They also found that this same region was activated during stimulation of the nipple, in addition to the region of SS devoted to the trunk (Komisaruk et al. 2011). The results of their earlier work on cortical activation across the entire time course of the female orgasm (i.e., from preorgasm tactile stimulation to postorgasm) were consistent with similar investigations, with the important finding that the vagus nerve could potentially provide an alternate pathway for genital stimulation. This would allow for sexual arousal that bypasses the spinal cord and activates areas such as the thalamus, amygdala, anterior cingulate, basal ganglia, cerebellum, and frontal, parietal, and insular cortices (Komisaruk et al. 2004; Komisaruk and Whipple 2005). Again, these responses have yet to be contextualized within a map of the entire body, although studying the sexual response over time begins to place it in context.

Finally, an alternate somatotopic localization for the human clitoris has been offered by Michels et al. (2010), who also used fMRI to map clitoral activity. Fifteen women (mean age = 26 years) were fitted bilaterally with 2 electrodes positioned on the clitoris to stimulate both sides of the dorsal clitoral nerve, a branch of the pudendal nerve. Eight participants also had an

electrode fitted to the inferior surface of their right hallux to serve as a reference point on SS. Stimulation of the clitoris revealed principally bilateral activation in dorsal S1 lateral to the representation of the toe, and in prefrontal cortex, precentral gyri, parietal operculum (S2), anterior putamen, posterior putamen and insula. A dominance of left-hemispheric activity in the bilateral activation was attributed to the viscerosensory innervation and processing function of the insula, which also demonstrated asymmetrical activation. The authors noted that there was a complete lack of activation on the medial wall of the postcentral gyrus (S1) during clitoral stimulation (Michels et al. 2010). This alternate location may be due to stimulation of the perineal or groin region, which is localized on a more superior and lateral portion of the paracentral lobule than the genitals (Komisaruk et al. 2011).

### Nonhuman Female SS: What Is Known

A review of research conducted on nonhuman animals provides the opportunity to explore maps of the breast, ventrum, and genitals generated using single electrode recordings, thereby providing both high resolution and precise localizations.

#### *Nonhuman Primates*

Somatotopy has been mapped in chimpanzees, gibbons, and macaques by direct physiological recordings (Woolsey and Bard 1943). While the sex of the animal goes unmentioned more often than not, those mapping studies that do consider the sex of the animal provide valuable information. Studies in chimpanzees and gibbons demonstrate that the genitals of both females and males are localized deep within and on the posterior wall of the central sulcus, continuous with the locations for the hip and trunk (Woolsey 1947; Woolsey et al. 1960; Woolsey 1964). These studies are in contrast to the human studies of Penfield and Rasmussen (1950), but support the later results of the study of Kell et al. (2005), which place the male genital representation lateral to that of the foot.

A detailed single-unit mapping study of the genitalia of 2 female macaque monkeys revealed somatotopic representations of the trunk and adjacent body regions, as well as of the genitals and glutea, in the anterior parietal SS (Brodmann areas 3b and 1). Representations of the feet, genitals, glutea, buttocks, thighs, trunk, neck, upper head, and arms of both females and males were mapped in a medial-to-lateral sequence (Rothmund et al. 2002). With respect to somatotopic location of the male genitalia, these findings differ from the human map of Penfield and Rasmussen (1950). However they concur in finding that only a small region of cortex is devoted to the genitalia and support Penfield's homunculus in that they find the male and female representations are in the same cortical locations. Although the findings of these investigations of nonhuman primates conflict with the Penfield homunculus, they are in agreement with more recent human fMRI studies showing alternate somatotopic representations of the genitalia (Kell et al. 2005; Michels et al. 2010).

#### *Rodents*

One question of interest with respect to the female SS is how the representation of different body regions might change with fluctuating hormone levels over the reproductive cycle or with reproductive experience. In S1, specifically, when the representation of the ventrum in S1 of virgin and lactating rats was

compared, the representation in lactating females was 1.6 times larger than that of controls; nipple-bearing skin had almost a 2-fold increase. In addition, the receptive fields of individual neurons in the map were significantly smaller for the lactating than for the virgin rats (Xerri et al. 1994). This may be due to the experience of nursing or hormonal changes pre- and postpartum. That SS might be affected by changes in estrogen levels is highly likely since estrogen receptors have been identified in female rat S1 (Zsarnovszky and Belcher 2001).

With respect to sex differences in noncortical activation following sexual activity, several researchers have found differences in early gene expression between males and females following stimulation of the genitals and during mating. In addition to differences in activation of SS, females show greater expression of c-fos in the medial preoptic area and amygdala, regions rich in estrogen receptors, compared with males (Pfaus et al. 1993; Wersinger et al. 1993). These dimorphic neural responses to mating behavior may be due to sex differences in sensory pathways, with the female having greater innervation from the pelvic nerve and the male having greater innervation from olfactory-vomer nasal pathways (Wersinger et al. 1993). Thus, not only are there different neural responses in areas activated by sexual behavior in both sexes but also different sensory pathways involved in relaying sexual information in males and females.

Sex differences in pain thresholds appear to depend on estrogens since the differences can be eliminated in female estrogen receptor knockout mice (Li et al. 2009). None of this is surprising, since numerous animal studies have demonstrated effects of estrogens on dendritic growth and synaptic density; results have consistently demonstrated that the phasic shifts in estradiol levels that accompany the menstrual cycle affect patterns and levels of neuronal activity most likely through the addition or reduction of synapses (Woolley 1998; Spencer et al. 2008). Of particular interest is a robust dendritic plasticity in the amygdala that is correlated with fluctuations in ovarian hormone levels, especially following pregnancy (Rasia-Filho et al. 2004). To our knowledge, the impact of pregnancy, delivery, and lactation on human female neocortex has not been studied.

### Accessory Areas to the Female SS

The insula and S2 may function as accessory areas to S1 in the female homunculus. The insular cortex consists of an anterior and a posterior region, both of which connect with much of cerebral cortex including various sensory association regions. On this basis, Kern et al. (2001) suggested that the insula might be considered a visceral sensory area, noting activation following upper and lower gastrointestinal tract stimulation and rectal distension in women. In men, there is an increase in rCBF bilaterally in S2 after stimulation of the penis (Kell et al. 2005) and in women, after stimulation of the vaginal vestibulum (Pukall et al. 2005). Other studies also support the hypothesis that the insula has a sensory processing function, especially for the viscera (Kern et al. 2001; Komisaruk et al. 2004; Komisaruk and Whipple 2005; Komisaruk et al. 2011; Eickhoff et al. 2006; Georgiadis et al. 2009; Michels et al. 2010). Insular stimulation (and resultant genital sensation) was likely omitted from Penfield's studies due to insufficient electrode penetration. Given that the greatest portion of the clitoris is internal (O'Connell et al. 2005), it may be that much of its representation is mapped to the insula. A full mapping of

female viscera may further implicate the insula in somatosensation.

In Penfield's homunculus, representations mapped to S1 and S2 are collapsed into one region suggesting that the genitalia may be partially represented in S2 (Penfield et al. 1951). S2 may also process additional cognitive and sensory aspects of genital stimulation, such as pain (Pukall et al. 2005), or the assignment of a conscious label to stimuli, for example, classifying genital stimulation as "sexual" (Georgiadis et al. 2006). S2 (the anterior portion of the parietal operculum) also contains a representation of the rectum and anus for both human males and females (Eickhoff et al. 2006).

The extent to which female genitals are internal, in comparison to those of males, suggests that the insula and S2 may play a greater role in the map of the genitals for females than it does for males. Komisaruk and colleagues identified regions in the insula activated during stimulation of the cervix in women with spinal cord injury above the level of entry of genitospinal sensory nerves; this finding indicates a sensory pathway to the cortex, which, unlike nerves carrying male genital sensation, does not go through the spinal cord (Komisaruk et al. 2004; Komisaruk and Whipple 2005). Thus, this group of researchers have offered an additional sensory processing pathway for the internal portions of the female genitalia, which would suggest a different mapping of the genitals in the cortex.

### Remapping after Surgery in Females

Somatosensory cortical remapping and reorganization following mastectomy and amputation have been demonstrated. Cortical remapping of the breast occurs in approximately 33% of female patients postmastectomy, a significant number of whom have referred sensation from their amputated breast and nipple when stimulated on ipsilateral body regions contiguous to the breast representation in the SS. These phantom sensations appear as early as 5 days following mastectomy and can persist for as long as 12 years postmastectomy (Aglioti et al. 1993; Aglioti, Cortese, et al. 1994). In a preliminary study using fMRI, the somatotopic representations of the human female breast pre- and postmastectomy were compared revealing a reduction in cortical representation of the amputated breast comparing pre- and postsurgery (Aurbach et al. 2009). The case of a woman with a lower leg amputation who reported phantom sensations upon stimulation of the rectum and anus also suggests remapping after trauma (Aglioti, Bonazzi, et al. 1994).

### Sex Differences in Neocortex

#### *Sex Differences due to Ovarian Steroids*

Ovarian steroids, principally estrogens and progestagens, have been correlated with changes in cortical regional glucose metabolism (RGM) as well as changes in cortical structure and function. Reiman and colleagues examined RGM in 10 women over the course of 2 full menstrual cycles. Two testing sessions were conducted, at which time the subjects provided blood samples to determine follicle-stimulating hormone, estradiol, and progesterone levels at the time of PET scans. This revealed significant differences in regional activation during the different phases of the menstrual cycle. During the mid-follicular phase, there was increased RGM in the thalamus, prefrontal cortex, temporoparietal and inferior temporal

regions. During the midluteal phase, there was increased RGM in the superior and anterior temporal, occipital, cingulate, anterior insular regions, and cerebellum (Reiman et al. 1996). In addition, the amount of gamma aminobutyric acid (GABA) in occipital lobe fluctuates with the ovarian cycle (Epperson et al. 2002) and changes in progesterone and allopregnanolone blood levels are associated with a form of depression common in women, Premenstrual Dysphoric Disorder (Epperson et al. 2002; Amin et al. 2006). The human hippocampus is also sensitive to the ovarian cycle, since catamenial epilepsy is entrained with changes in estrogens and progestagens (Herzog 2008; Quigg et al. 2008). Different types of pain response vary across the menstrual cycle with higher thresholds to pressure, cold, hot thermal pain, and ischemic muscle pain during the follicular phase and higher thresholds to pain from electrical stimulation during the luteal phase (Riley et al. 1999). Taken together, these suggest that the female somatosensory map might vary with different reproductive stages, a physiological case not represented by Penfield's homunculus.

### **Sex Differences in Cortical Representation**

That there is a necessity to study somatosensory mapping in females as well as males is underscored by the fact that when structure, biochemistry, and behavior of the female and male nervous systems are compared, significant differences are often found (Wizeman and Pardu 2001; Cahill 2006; Becker 2008; Cosgrove et al. 2007; Einstein 2007). This should not come as a surprise, since studies have shown the impact of hormones and sex differences on neuronal growth and density from the time when the nervous system is forming in utero (e.g., Chen et al. 2009; Kordower et al. 2010). In studies in which adult female and male cortical responses to sensory stimulation have been compared directly, sex differences are often observed in both the healthy and the diseased nervous system (Cahill 2006).

With respect to sensory processing of viscera, there are demonstrated sex differences in cortical activation with rectal distension; while in both sexes, rectal distension was correlated with a progressive increase in total cortical activity, cortical activity was significantly higher in women. As well, while both males and females showed clusters of activation in the sensory and parietooccipital cortex, only females showed significant activation in anterior cingulate and insular regions (Kern et al. 2001). There are also sex differences in cortical activation during tactile genital stimulation; rCBF differs significantly between women and men; there is decreased rCBF in the neocortex during female orgasm but not male (Georgiadis et al. 2009).

Although some studies show a similar somatotopy for genital sensation in females and males (Rothenmund et al. 2002; Kell et al. 2005; Michels et al. 2010), there are others who find sex differences in genital localizations. Komisaruk et al. (2011) demonstrated that the vagina, cervix, and clitoris each have their own distinct somatotopic representation. They hypothesized that this difference is due to the fact that the vagina, clitoris, and cervix are each separately innervated by the pudendal, hypogastric, pelvic, and vagus nerves, respectively (Komisaruk et al. 2004; Komisaruk and Whipple 2005; Komisaruk et al. 2011). While the authors note individual variability in their fMRI data, these studies are a very important step toward understanding the innervation and processing of sensory inputs from the female genitalia that might lead to

sex differences in cortical representation (Komisaruk et al. 2011). Taken together, these findings provide further evidence for differential sensory processing not only between the sexes but also of internal and external sacral structures among females.

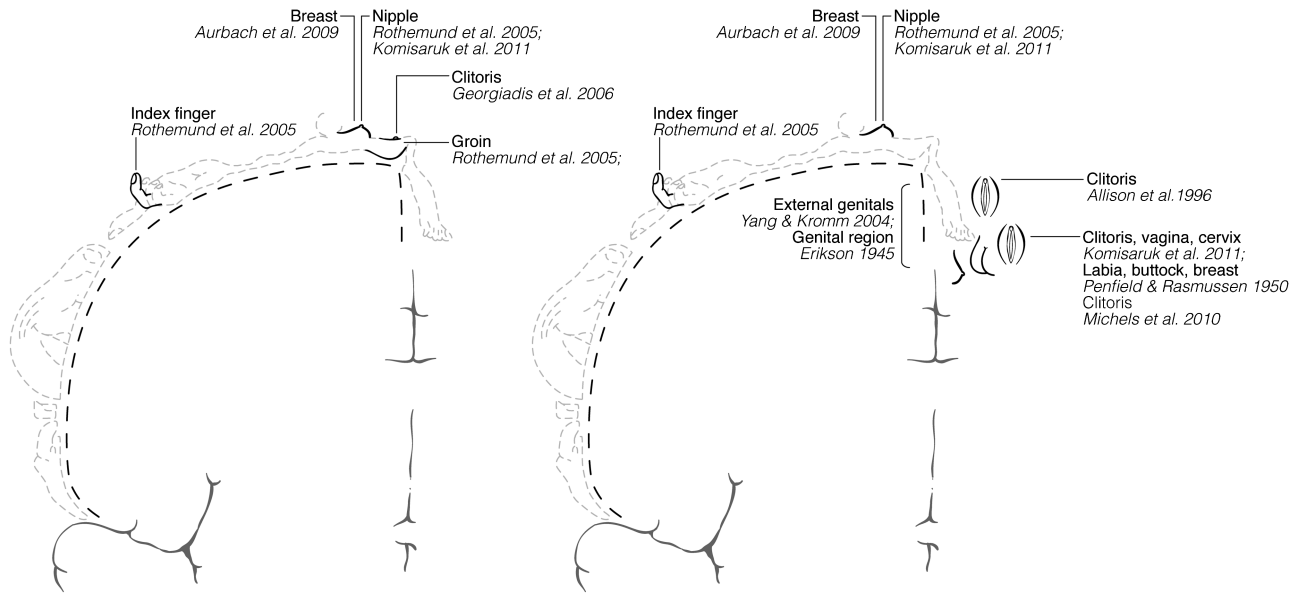
### **Why Is Not There a *Hermunculus*?**

Given these differences in anatomy and innervation, one would expect that the male and female somatotopic maps would differ. Why is not there a map of the female body in the brain—a *hermunculus*? While Penfield and his colleagues stimulated the cortices of female patients, these represent only approximately 10% of his experimental population, and there is scant discussion of the responses of these women. This leaves a serious gap in our knowledge about somatosensory representation, remapping, and plasticity due to hormones as well as experience.

Perhaps the most obvious reason for avoiding examinations of female genital representation in the cortex stems from the social taboos and connotations associated with such a research question. One need look no further than the title of the case study of Erickson (1945) of an “erotomaniac” female patient whose seizures included sensations of the vagina and labium. The objectivity with which this patient's epilepsy was examined is undoubtedly clouded by social restrictions of the time, as the expression “eroticism” is itself a socially charged and subjective term. We can extend this commentary on social expectations to Penfield's examinations of female subjects, who may have felt embarrassed about reporting genital sensations to men of authority. Even the medical professionals conducting these studies were careful to distinguish reports of genital sensations as strictly asexual; for instance, Penfield and Rasmussen (1950) made it very clear that there was nothing in patient E.C.'s reported sensation that resembled sexual excitement, suggesting the possibility of forfeiting objectivity for the sake of social correctness.

In Penfield's case, the dearth of female patients might also have obscured sex differences due to a compression of ages, reproductive status, and/or menstrual phases. Additionally, Penfield's patients had epilepsy, a condition which might have led to a remapping of various cortical areas. Finally, the purpose of Penfield's studies was to localize the foci of seizure onset. Using direct electrical cortical stimulation, he would explore the cortical space exposed during surgery until a seizure was induced, and the area of cortex that he deemed responsible for mediating these epileptic seizures would be excised. He used high current, which might have recruited neurons at a distance from the electrode and thus obscured the precise location of a given body region.

A number of contemporary studies using more precise neuroimaging methods have presented evidence that the somatotopy of different body regions may differ somewhat from Penfield's rendering in both human and animal models. For example, even when using unconventionally low statistical thresholds, Kell et al. (2005) found no indication of a penile representation in the paracentral lobule. The close proximity of trunk, penis, and leg representations in SS suggests that stimulation of several areas simultaneously might account for Penfield and Rasmussen's finding that fewer than 1% of the patients, both male and female, reported any distinct genital sensation (Penfield and Rasmussen 1950).



**Figure 2.** Two versions of the somatosensory homunculus, depicting findings from human female mapping studies and showing alternative localizations for the genitalia. Left depicts the genitalia mapped to the dorsal somatosensory cortex and right depicts the genital representation mapped along the medial wall. Penfield's homunculus (shown with a gray dashed outline) is included to provide context and to demonstrate how much of the female SS remains unmapped. These illustrations are conceptual: the extent and location of each representation are not precise.

### Beyond Penfield

The study of sex differences, especially in the brain, suggests that there will be differences between the female and male maps (Cahill 2006; Einstein 2007). As mentioned, obvious anatomical sex differences also make it likely that the brain map of the body will differ. Functional and physiological differences between females and males also support this hypothesis. Despite their common innervation by the pudendal and dorsal nerves (Guérit and Opsomer 1991) and their origin in the same embryonic tissue, the clitoris and penis as well as the female and male rectum elicit different patterns of rCBF and brain activation during anal stimulation, genital stimulation, and orgasm (Kern et al. 2001; Georgiadis et al. 2006).

Studies in rodents as well as in humans have demonstrated cortical and dendritic plasticity based on female life experiences such as nursing (Xerri et al. 1994), mastectomy (Aurbach et al. 2009), lower limb amputation (Aglioti, Bonazzi, et al. 1994), and the fluctuation of ovarian steroids over the menstrual cycle (Woolley 1998; Riley et al. 1999; Epperson et al. 2002; Rasia-Filho et al. 2004; Amin et al. 2006; Reiman et al. 1996; Quigg et al. 2008; Spencer et al. 2008; Li et al. 2009; Rhudy and Bartley 2010). The resilience of female orgasm following spinal cord injury (Komisaruk et al. 2004; Komisaruk and Whipple 2005) would imply sex differences in the cortical map beyond sexual function.

In addition to producing a map of female SS, one might suspect that there are reasons to revisit Penfield's original homunculus in order to better understand the representation of the male body in the brain as well. Penfield's map was produced by stimulating with a relatively high current, which may have excited regions at a distance from the electrode. As well, his patients had intractable epilepsy and may have had remapping due to neuronal damage from seizures. Given the technological limitations of his time, the motivation to localize function, study a population with an existing neurological disorder, and a general lack of appreciation for cortical

plasticity throughout life, Penfield's map may omit many important aspects of somatosensory mapping for both males and females. Newer, more sensitive methods may contribute more fully to our knowledge. For example, local neurological activity that results from electrical stimulation of nerves can be measured with fair sensitivity and good spatial localization with scalp arrays (electroencephalogram). Using this method, evoked action potentials originating in the postcentral gyrus called Somatosensory Evoked Potentials (SSEPs) can be combined with MRI to localize body regions in the brain (Rothmund et al. 2005). Several types of functional imaging methods with high spatial resolution are also available, and these offer the ability to measure changes in cortical activity *over time*—something Penfield was never able to accomplish. PET and fMRI both provide measures of event-related regional cortical activation over time by measuring blood flow to the active region as, for example, during orgasm (Komisaruk et al. 2011). The blood oxygen level-dependent (BOLD) signal that emanates from blood flow changes in fMRI provides high resolution of both temporal and spatial information. Additionally, these are noninvasive measures allowing changes due to hormones and experience to be mapped over multiple sessions. Thus, newer methods not only allow for greater precision in mapping healthy individuals but provide a route to study individual changes over a lifetime which may reveal substantial variation both between men and women as well as within a given individual.

In fact, in many cases, when mapping is redone using modern methods, the results vary from Penfield's. Using fMRI, the somatosensory cortices of 8 healthy male volunteers were scanned during resting state and during stimulation of the left prepuce and proximal-to-distal portions of the left penile shaft. As controls, the left hallux and left lateral abdominal wall were also stimulated. In this way, the study established the penile representation in its entirety as well as its relationship to more lateral sensory foci. The authors report that no physical sexual

responses were elicited and no sexual feelings were reported. Thus the results can be interpreted as sensory, not sexual, processing. Significant activation was found in SS within either Brodmann area 1 or Brodmann area 3b with the penile tip and shaft represented lateral to the representation of the toe. The primary penile representation overlapped with that of the lower abdominal wall. Interestingly, the exact location of sensory foci varied among participants but all had the same somatotopic sequence from medial to lateral: toe, lower abdomen, and penis (Kell et al. 2005). This is in contrast to the sequence proposed by Penfield and Rasmussen (1950), but in agreement with the recent findings in nonhuman primates (Rothmund et al. 2002), and suggests that male body somatotopy might vary between persons, life stages, sexualities, health, and illness. Thus, the homunculus as a representation of the male body map might also benefit from reconsideration.

### What Would the Hermunculus Look Like?

So what kind of a map of the female body in the brain does research since Penfield's reveal, and what can it tell us about an explicitly female somatotopic map? The results cluster into 2 alternative versions of the partial hermunculus (Fig. 2). One version locates the genitals in the medial wall of the cerebral hemisphere, as in the original homunculus (Erickson 1945; Penfield and Rasmussen 1950; Allison et al. 1996; Yang and Kromm 2004; Komisaruk et al. 2011). The other locates the genitals and groin region lateral to the interhemispheric fissure, on the dorsal surface of the cerebrum (Rothmund et al. 2005; Georgiadis et al. 2006; Michels et al. 2010). The female breast and nipple appear to be represented on the dorsal surface as well, in the region identified with the male chest by Penfield (Rothmund et al. 2005; Aurbach et al. 2009; Komisaruk et al. 2011). Komisaruk et al. (2011) observed that stimulation of the nipple elicited concurrent activation of the genital region on the medial wall, and that stimulation of the vagina also elicited activation of the thoracic nipple region. A representation of the vagina also exists in S2 (Pukall et al. 2005). In addition, the insula has also been widely implicated as a potential accessory region for the female somatosensory map (Kern et al. 2001; Komisaruk et al. 2004; Komisaruk and Whipple 2005; Komisaruk et al. 2011; Eickhoff et al. 2006; Georgiadis et al. 2009; Michels et al. 2010) (Fig. 2, Table 1).

As Figure 2 makes clear, current female-specific somatotopic mappings focus fairly exclusively on the genitalia and sexual function of women, and a static one at that. Thus, even our contemporary knowledge of the female body in the brain remains fragmentary; much remains to be mapped if we are to arrive at a hermunculus that reflects the totality of women's bodies and the effects of female life cycles and experiences.

### Conclusion

Through his studies of localization of function, Wilder Penfield gave us a vibrant figure by which to visualize the representation of the body in the brain. This figure, the homunculus, has underpinned our understanding of bodily sensation ever since. However, it is an understanding predicated on the male body as representative of all bodies. Recent research has sought to redress the exclusion of female bodies from the somatotopic map and to incorporate insights based on more sensitive contemporary imaging techniques and on a neuroscience

informed by new ideas about adult brain plasticity. However, it still presents a relatively incomplete picture of the female body.

To advance knowledge, as well as for potential therapeutic purposes, we propose that the female somatosensory map be filled in to include the rest of the body. The implications of this map for understanding sensation over a variety of women's and men's life stages are hugely important. What happens to bodily sensation during pregnancy, menopause, normal aging, and neurodegenerative disease, or after surgeries such as oophorectomy, prostatectomy, heart and kidney transplants? Given the often poor outcomes, including chronic pain, it might be of particular interest to understand changes in cortical maps following cosmetic surgeries such as breast implants, labia reduction, and traditional practices such as female genital mutilation/circumcision/cutting (Einstein 2008). The resulting hermunculus—a complete and explicitly female body representation—could then take its place alongside an updated male homunculus in the catalog of neuroscientific iconography and therapeutic resources.

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### Notes

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