An isomorphic three-dimensional cortical model of the pig rostrum

Cindy Ritter1 | Eduard Maier1 | Undine Schneeweß1 | Tanja Wölk1 | Jean Simonnet1 | Safaa Malkawi1 | Lennart Eigen1 | Elcin Tunckol1 | Leopold Purkart1 | Michael Brecht1,2

Bernstein Center for Computational Neuroscience Berlin, Humboldt-Universität zu Berlin, Berlin, Germany
NeuroCure Cluster of Excellence, Humboldt-Universität zu Berlin, Berlin, Germany

Correspondence
Michael Brecht, Bernstein Center for Computational Neuroscience Berlin, Humboldt-Universität zu Berlin, Philippstr. 13, Haus 6, 10115 Berlin, Germany.
Email: michael.brecht@bccn-berlin.de

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Abstract
Physiological studies of the last century mapped a somatosensory cortical gyrus representing the pig's rostrum. Here, we describe the extraordinary correspondence of this gyrus to the rostrum. The pig rostrum is packed with microvibrissae (~470 per hemi-rostrum) and innervated by a prominent infraorbital nerve, containing about 80,000 axons. The pig's rostrum has three major skin-folds. The nostrils have a rectangular medial wall and a funnel-like lateral opening, nasal channels run obliquely from lateral (surface) to medial (inside). The rostrum gyrus mimics rostrum geometry in great detail. The putative representation of skin folds coincides with blood sinus and folds of the rostrum gyrus. The putative nostril representation is an oblique sulcus running from lateral (surface) to medial (inside). As observed in rodents, Layer 4 is thin in the nostril sulcus. The side of the nostril sulcus representing the medial wall of the nostril is rectangular, whereas the side of the nostril sulcus representing the lateral wall is funnel-like. Proportions and geometry of the rostrum and the rostrum gyrus are similar, albeit with a collapsed nostril and a larger interindividual variability in the gyrus. The pig's cortical rostrum gyrus receives dense thalamic innervation, has a thin Layer 1 and contains roughly 8 million neurons. With all that, the rostrum gyrus looks like a model of the pig rostrum at a scale of ~1:2. Our findings are reminiscent of the raccoon cortex with its forepaw-like somatosensory forepaw-representation. Representing highly relevant afferents in three-dimensional body-part-models might facilitate isomorphic cortical computations in large-brained tactile specialists.

KEYWORDS
isomorphic, pig, rooting, somatosensory cortex

1 | INTRODUCTION

Pigs are highly successful mammals. Pigs do not only form a major share of feral large mammals in their European and Asian areas of origin, but also are a most prominent invasive species in many parts of...
closely linked to their ability to sort through a variety of food items. The steady rooting activity of pigs has a major impact on soil structure and fertility (Sweitzer & Van Vuren, 2002). Specifically, it appears that pigs were domesticated first in the Near East, but that initial near-eastern-stock got gradually replaced by European wild boars (Ottoni et al., 2013). The ecological success of pigs is tightly related to a set of morphological and behavioral specialization of these animals. The most conspicuous feature of pigs is their prominent rostrum. The facial morphology is highly derived with a lengthening of the snout and a very prominent rhinarium. The pig rostrum is highly mobile and deformable and such mobility is supported by a complex musculature (Herring, 1972). In awake pigs, the rostrum is almost always in motion and is usually kept closely to the ground. A signature activity of pigs is their rooting behavior, that is, ramming their rostrum in the ground and skimming the ground for a wide variety of food items. The steady rooting activity of pigs has a major impact on soil structure and fertility (Sweitzer & Van Vuren, 2002). The dwelling of pigs on a wide variety of food sources appears to be closely linked to their ability to sort through “dirt” with their rostrum. Such food searching and sorting occurs as interplay between the pig’s excellent sense of smell and its tactile sensitivity. Indeed, such combined abilities have led to the deployment of these animals as truffle pigs.

While the omnivorous pigs are widely used in biomedical research for their metabolic similarities to humans, the sensory abilities of these animals have not been studied in depth by neuroscientists. We are interested in the large representation of the pig rostrum in the somatosensory cortex, as described by Lord Adrian’s early work (Adrian, 1943) and later confirmed and extended by Craner and Ray (1991) in newborn piglets.

The anatomy of somatosensory cortex has been extensively studied in the whisker/barrel cortex of rodents, where researchers were impressed with the exquisite topography of the barrel system (Woolsey & Van der Loos, 1970). The somatosensory cortex of primates has also been studied in great detail. While physiological studies in humans (Penfield & Rasmussen, 1952) and monkeys (Woolsey, 1958) initially identified one large somatosensory representation, subsequent microelectrode analysis showed multiple somatotopic maps (Areas 1, 2, 3a, 3b) with distinct receptive field properties (Kaas et al., 1979). This fine-grain division of the somatosensory cortex was in line with anatomical divisions proposed earlier (Brodmann, 1909). High-resolution anatomical analysis subsequently observed so-called finger isomorphs in monkeys (Jain et al., 1998).

While there are several thousands of studies on each the rodent whisker/barrel cortex and the primate somatosensory cortex, we know only little about the diversity of mammalian somatosensory cortices. In particular, we know little about high-performance tactile abilities outside of rodents and primates.

Here we study the anatomy of the rostrum gyrus of the domestic pig (Sus scrofa domesticus). Our anatomical analysis of the pig rostrum gyrus builds on the physiological identification of this brain structure by extracellular recording techniques in the last century. Because our anatomical results cannot be fully appreciated without such physiological data, we briefly show some of this work here. A pioneering contribution came from Lord Adrian (Adrian, 1943). Specifically, Adrian identified a prominent representation of the pig’s rostrum (Figure 1(a)) in a gyrus of the pig’s cortex (Figure 1(b)). This result was highly reproducible and Adrian obtained the same findings in a second animal (not shown). Almost five decades later, Craner and Ray (1991) reinvestigated the issue in a physiological study of the newborn piglet. They also observed a systematic representation of the rostrum—as indicated in their receptive field schematic (Figure 1(c))—in the pig’s cortex (Figure 1(d)) and their results (Craner & Ray, 1991) match very well Lord Adrian’s observations. Craner and Ray (1991) investigated a large number of piglets and observed a highly consistent mapping of the snout onto the rostrum gyrus, the topography of which they summarized as shown in Figure 1(e).

Specifically, we address the following questions: (a) What is the sensory layout of the rostrum? (b) What is the cytoarchitectonic organization of the rostrum gyrus? (c) How is the rostrum gyrus related to the pig rostrum? (d) How does the pig rostrum gyrus compare to rodent barrel and monkey finger cortex? We find that the pig rostrum gyrus is an extraordinarily large and precisely isomorphic ~1:2 sized model of the pig rostrum.

2 MATERIALS AND METHODS

2.1 Pig brains, snouts, and tissue

Brains of adult domestic pigs (Sus scrofa domesticus) were purchased from a local slaughterhouse. Exact age and sex of the animals was not known. Four pig brains and pig rostra were removed from entire pig heads; these specimens were used to match rostrum and brain in individual animals. The rostrum gyrus in the pig cortex (Figure 1) was readily apparent in all pig cortical hemispheres studied (n > 40).

2.2 Photography

A subset of cortical hemispheres (n = 15) were more closely investigated. All hemispheres were photographed with a Sony camera α7R/α7 before and after the arachnoidea had been removed. For high magnifications images we photographed with a tripod using a macro objective (FE 2.8/90 Macro G OSS; Ø82 0.28 m/0.92 ft) and for bigger tissue a wide angle objective (FE 2.8/16–35 GM; Ø82 0.28 m/0.92 ft). We also took photographs of the pig rostrum from entire pig heads.

2.3 Microfocus computed tomography

The internal structure of one pig rostrum was visualized with a micro-computed tomography (micro-CT) scan. To this end, the rostrum of an
An adult pig was dissected from the pig’s head and fixed for 2 days in 4% paraformaldehyde (PFA) in 0.1 M phosphate buffer (4% PFA). To enhance the contrast of the soft tissues, the specimen was stained with phosphotungstic acid as follows: 1 h in a water bath, 1 h in 15% ethanol, 1 h in 30% ethanol, 1 h in 50% ethanol, 1 h in 60% ethanol, and 1 h in 70% ethanol (Metscher, 2009a, 2009b). Then, it was placed in PTA (1% [wt/vol] phosphotungstic acid in 70% ethanol) for 28 days, which serves as a contrast agent (Koç et al., 2019).

The pig rostrum was scanned at the Museum für Naturkunde Berlin, with an YXLON FF35 CT (YXLON International GmbH; Essener Bogen 15, 22419 Hamburg, Germany). A helix scan with a detector time of 0.8 s was applied. Then, 1688 pictures were taken with a voxel size of 0.0533 mm × 0.0533 mm × 0.0533 mm. The scan parameters were 135 μA and 170 kV.

### 2.4 Fixation and sectioning

Pig brains were fixed for 2 days in 2 or 4% PFA in 0.1 M phosphate buffer. Specifically, we used a 2% PFA solution in cases, where we planned to perform a histochemical staining for cytochrome-c-oxidase reactivity staining (see below).Brains were sectioned (in most cases into 100 μm sections on a vibratome (Mikrom HM 650 V; Thermo Scientific). In some cases (n = 8), the rostrum gyri were manually flattened, cut tangentially parallel to the pia, into 100 or 150 μm thick sections and then processed.

We also dissected out two pig rostra from entire pig heads. Here, we dissected out the infraorbital nerve, which innervates the rostrum. We cut sections from the rostrum skin and investigated these microscopically.

### 2.5 Histochemistry

Sections were processed for Nissl substance, cytochrome oxidase reactivity (Wong & Kaas, 2008). Six complete series of tangential sections were stained for Nissl and cytochrome oxidase. Two complete series of parasagittal sections were stained for Nissl and cytochrome oxidase. Five complete series of coronal sections stained for Nissl substance or alternatingly for Nissl, cytochrome oxidase, and antibody stains (see below) were used for quantitative studies as detailed below.
FIGURE 2  Legend on next page.
2.6 | Immunohistochemistry/antibody characterization

One series of coronal sections was stained for neuronal somata with rabbit anti-neuronal nuclei I (NeuN) antibody (Merck, Catalog Nr. ABN78A4, Lot Nr. 3209767), which we used at a dilution of 1:1000. Staining of sections through the cerebral cortex produced a pattern of neuronal somata as expected from previous descriptions Lind et al. (2005).

Series of sections were processed, alternating with Nissl, cytochrome oxidase and antibody staining. Typically, we stained every sixth 100 μm section for either staining, remaining sections were discarded. Sections were cut either coronally or semiparasagittally along the longitudinal axis of the rostrum gyrus. Antibody stains included VGluT2 with mouse anti-vesicular glutamate transporter 2 (VGluT2) antibody. This purified monoclonal antibody (Millipore, Catalog Nr. MAB5504, Lot Nr. 3015311), which we used at a dilution of 1:1000, was raised against recombinant protein from rat VGluT2. VGluT2 is a marker for thalamocortical projections to sensory cortex (Fujiyama et al., 2001) and the staining pattern in cerebral cortex corresponds to what would be expected from previous studies using this antibody in other species and previous studies of thalamocortical projections in insectivores (Ebner, 1969; Valverde et al., 1986). Sections were processed for NeuN. Briefly, sections were incubated in a blocker of 0.1 M PBS, pH 7.2, with 0.5% Triton X-100 and 5% normal horse serum for an hour at room temperature before incubation in their respective primary antibodies (see description in text) in the blocker for 48 h at 4 °C. After rinsing, the sections were incubated in the blocker containing secondary donkey anti-mouse antibody conjugated to Alexa Fluor 546 (1:200; Invitrogen, Catalog Nr. A10036, Lot Nr. 1977695) and secondary donkey anti-rabbit antibody conjugated to Alexa Fluor 488 (1:200; Invitrogen, Catalog Nr. A21206) overnight. The next day sections were washed, mounted and then coverslipped with mounting medium (Fluoromount; Biozol, Eching, Germany).

2.7 | Golgi staining

For Golgi staining, brains were only minimally fixated (1 day 1% PFA in 0.1 M phosphate buffer). Staining was performed with a commercial kit (Rapid Golgi Kit, Gentaur, Aachen Germany). Sections for Golgi staining were cut at a thickness of 200 μm.

2.8 | Light microscopy and anatomical reconstruction

Cortical region borders were detected by laminar and cell density changes in the sections that have been processed for Nissl, cytochrome oxidase, and myelin stainings. Nissl, myelin, and cytochrome oxidase stained sections were useful for differentiating distinct sets of cortical fields.

Nissl sections allowed to distinguish cortical regions and were used to identify cortical layers, determine their thickness and their cell density, as well as individual cell size and shape. Myelin and cytochrome oxidase stains were evaluated for staining pattern and intensity. In general, the different histological procedures revealed almost identical boundaries.

Processed sections were viewed with the Stereo Investigator software (MBF Bioscience, Williston, ND) employing an Olympus BX51 microscope (Olympus, Japan) with a MBF CX9000 camera (MBF Bioscience) mounted on the microscope. The microscope was equipped with a motorized stage (LUDCX9000 camera (MBF Bioscience) mounted on the microscope. The microscope was equipped with a motorized stage (LUDL Electronics, Hawthorne, CA) and a z-encoder (Heidenhain, Schaumburg, IL). Stereo Investigator was used for stereological procedures and acquiring images. Digitized images were adjusted for brightness and contrast using Adobe Photoshop (Adobe Systems Inc., San Jose, CA), but they were not otherwise altered.

2.9 | Layer 4 flat map

We first attempted to generate a flat map of Layer 4 in the rostrum gyrus by flattening gyri and staining them for cytochrome-oxidase reactivity, as described above. Given the deep and narrow middle sulcus, however, we found it impossible to flatten the gyri, such that Layer 4 was contained in a single or a few tangential gyral sections. We, therefore, decided to generate a Layer 4 flat map digitally from data derived from serial coronal sections. To this end, we made drawings of Layer 4 in the rostrum gyrus in serial coronal sections. The Layer 4 of the rostrum gyrus is distinct with a very strong cytochrome-oxidase reactivity as shown in the micrograph/drawings in Figure 5. We drew Layer 4 in all coronal sections of the rostrum and measured the thickness of Layer 4 using the Neurolucida software (MBF Bioscience) across the mediolateral extent of the gyrus. Thus, we obtained for each section a set of thickness values across the mediolateral extent of the gyrus. We aligned section to the lateral end.

FIGURE 2 The pig rostrum. (a) Frontal view. The snout has been brushed; the location of microvibrissae can be seen as dots. (b) Drawing of the rostrum with major skin folds and microvibrissae. (c) High magnification photograph of the dense microvibrissae on the lower rostrum (field of view as indicated in (b)). (d) Exposed blood sinus of a microvibrissa. (e) Surface rendered image of a micro-computed tomography (CT) of a pig rostrum stained with phosphotungstic acid. (f) Horizontal section (plane of section is indicated in (e) by the dashed line) through a micro-CT volume of a pig rostrum stained with phosphotungstic acid. C = caudal; L = lateral. (g) High magnification view of a micro-CT section directly below the skin (indicated by the small dashed square in (e)) of a pig rostrum stained with phosphotungstic acid. Blood sinus of microvibrissae and a mesh of muscle fibers can be recognized. (h) Coronal section (indicated by the large dashed square in (e)) through a micro-CT volume of a pig rostrum stained with phosphotungstic acid. D = dorsal; M = medial.
FIGURE 3  Legend on next page.
of the rostrum layer, which corresponds to representation of the rostrum midline. For presenting the Layer 4 flat map we coded Layer 4 thickness in gray values. Because we kept only every 6th section, we “filled” the empty space between those sections by interpolating Layer 4 thickness data-points in the anterior–posterior direction.

### 2.10 Infraorbital nerve preparation and staining

Staining procedures for infraorbital nerve staining and visualization were performed analogous to the nerve staining procedures optimized for axon counts described in Purkart et al. (2020). Infraorbital nerves (n = 3) were dissected out from commercially obtained adult pig heads (n = 2). Nerves were cleaned from connective tissue and stored in a 4% PFA in 0.1 M phosphate buffer solution for ~24 h. The solution was then changed to 70% ethanol for paraffin embedding. The tissue was transferred to a Hypercenter XP Tissue processing system, running an ascending alcohol series. Next, the nerve segments were kept in a furnace at 60°C for 24 h and embedded in paraffin blocks using the Leica EG 1160. Blocks were cut into 8 μm sections, which were left to float in a 45°C preheated water-bath. The sections were then mounted on Thermo Scientific Superfrost Ultra Plus GOLD slides and stored overnight in a furnace at 42°C. Before applying the immunohistochemistry protocol, sections were deparaffinized and rehydrated in a descending ethanol series. For immunohistochemical staining of infraorbital nerves, we performed heat-induced epitope retrieval using a citrate buffer (Antigen Unmasking Solution, Citric Acid Based, pH 6, x100 concentrated stock solution, Vector Laboratories Cat# H-3301, RRID: AB_2336227). A water-bath with a staining dish, containing the antigen retrieval solution, was preheated to 95–100°C. Mounted sections were placed in the dish, heated for ~60 min and left to cool for 30 min at room temperature. Antibody staining was performed according to standard procedures. In summary, nerve sections were pre-incubated for an hour at room temperature in a blocking solution (0.1 M PBS, 2.5% bovine serum albumin and 0.5% Triton X-100). Afterwards, primary antibodies were diluted in a solution containing 0.5% Triton X-100 and 1% bovine serum albumin. We prepared nerve fiber stains with a primary antibody against Neurofilament H as specified below; the antibody stain led to complete and fully analyzable staining patterns of the infraorbital nerve. The primary antibody against Neurofilament H (Chicken polyclonal, Millipore Cat# AB5539, RRID:AB_11212161) was incubated for at least 48 h under gentle agitation at 4°C. Incubation with the primary antibody was followed by detection with a secondary antibody, coupled to the fluorophore Alexa 488 (Goat anti chicken: Thermo Fisher Scientific Cat# A-11039, RRID:AB_2534096). The secondary antibody was diluted (1:1000) in 1% bovine serum albumin in 0.1 M PBS and the reaction was allowed to proceed overnight in the dark at 4°C. To stain myelin sheaths in the infraorbital nerve, we placed deparaffinized slides in 1% Luxol Fast Blue solution at 56°C for 24 h followed by differentiation in 0.05% lithium carbonate. We covered the mounted nerve sections with Fluormount G (Biotrol) mounting medium. Z-stacks were taken on a Leica DM5500B epifluorescence microscope with a ×63 oil lens (axial resolution 0.772 μm). The z-planes were 0.1 and 1 μm apart, respectively. The images obtained were from 2937 × 3509 to 5811 × 7615 pixels in size with a field of view between 372 × 445 μm and 737 × 966 μm. Stacks were analyzed using ImageJ (RRID:SCR_003070).

### 2.11 Stereology

We estimated the total number of neurons in the rostrum gyrus using stereology methods. We estimated the total number with Stereo Investigator software (MBF Bioscience) using a sampling scheme called the optical fractionator method. Our region of interest was identified and outlined at low magnifications. The neurons were identified by their shape and staining intensity at high magnification (Oil, x100, numerical aperture 1.25) and counted individually. The standard stereological sampling scheme is independent of volume, measurements and shrinkage because the number of neurons is estimated directly without referring to neuron densities. Using the optical fractionator technique, we counted the nucleoli that come into focus and fall within the acceptance lines of the dissector, which were randomly placed on the series of sections (Howard & Reed, 2005; Naumann et al., 2012; West & Gundersen, 1990). We counted neurons in two rostrum gyri. The first gyrus was stained with Nissl substance and sliced at 100 μm. The second was stained with a NeuN-antibody visualized with biotinated secondary antibody /a DAB (3,3’-diaminobenzidine) precipitate and sliced at 80 μm thickness. In the first gyrus, we counted fewer sections but more sites and more neurons per site. In the second NeuN-stained gyrus we analyzed more sections but fewer sites and fewer neurons counted per site. Specifically, we used the following parameters in this case. The dissector laid a grid of squares over our region of interest with a size of 1000 × 600 μm², where we counted the neurons at each dissector in the counting.

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**FIGURE 3** Rostrum innervation by the pig infraorbital nerve. (a) Left pig infraorbital nerve. (b) Cross section of the infraorbital nerve. Fifty-four fiber bundles are revealed by anti-neurofilament-antibody staining (green fluorescence). (c) High magnification epifluorescence micrograph of one fiber bundle. Single axon stained by anti-neurofilament-antibody can be readily resolved. (d) High magnification micrograph of one fiber bundle stained by luxol-fast-blue to reveal myelin sheaths. (e) Fiber counts of five (of the 54) fiber bundles were made. Counts correlated well with the cross-sectional area of the fiber bundle. Based the total cross-sectional area, we estimate this left pig infraorbital nerve contained ~81,000 axons. In the same way, we arrived at an estimate of ~78,200 axons for the right infraorbital nerve of this pig. (f) Fiber counts (according to anti-neurofilament-antibody staining) versus counts of myelin sheaths (according to luxol-fast-blue staining) for five fiber bundles. The counts are strongly correlated. Fiber counts are consistently higher than myelin sheath counts and slope of 1.2 of the regression line suggests that about 83% of infraorbital nerve fibers are myelinated.
FIGURE 4 Legend on next page.
frame area of $40 \times 30 \mu m^2$. At each counting frame, we counted between one and three neurons, which is considered optimal for this counting procedure (Howard & Reed, 2005). More than 700 neurons were counted for assessing the total number of neurons. We sectioned at 80 \mu m thickness and stained every 6th section alternately for Nissl substance and biotinylated antibody. The entire gyrus was contained in 324 sections, every 18th section was counted. The thickness of the mounted sections was measured in advance and found to be around 66.9 \mu m. A guard zone of 6 \mu m above and below the counting volume was used. Guard zones are regions in the z-axis that form the upper and lower boundaries for the counting volume; neurons falling within these zones are not counted (Naumann et al., 2012). The mean thickness measured at every counting site was measured to be around 61.2 \mu m and used to estimate the total number of neurons.

3 | RESULTS

3.1 | The pig rostrum

The pig rostrum is a sensory/motor organ with vibrissae and skin mediating touch, nostrils mediating smell, and is packed with muscles mediating its extraordinary motility. A frontal view of the pig rostrum is shown in Figure 2(a). As captured in the drawing shown in Figure 2(b), the rostrum is covered by about 900 vibrissae (889, 975, and 929, respectively, in the three rostra studied). The drawing also highlights the three prominent skin folds of the pig rostrum: a lateral fold, which curves upward, a horizontal fold between the two nostrils and a vertical midline fold. In some parts of the rostrum the microvibrissae are densely spaced (Figure 2(c)). The microvibrissae are true vibrissae/sinus hairs, as indicated by the presence of a prominent blood sinus (Figure 2(d)). To obtain a better understanding of the internal organization of the pig rostrum, we stained a pig rostrum with phosphotungstic acid and performed a microfocus CT (Figure 2(e–h)). The horizontal image plane reveals the nostril geometry (Figure 2(f)). Directly below the frontal skin a dense mesh of muscle fibers surrounding blood sinus of microvibrissae is observed (Figure 2(g)). A coronal section reveals the dense packing of microvibrissae follicles in some parts of the rostrum and also deeper lying muscles (Figure 2(h)).

We conclude that the pig rostrum has a stereotyped layout of skin folds and is packed with microvibrissae.

3.2 | Characterization of rostrum innervation by the pig infraorbital nerve

To obtain a first assessment of the sensory innervation of the pig rostrum we prepared the pig infraorbital nerve, a sensory nerve with a huge diameter (Figure 3(a)). We then prepared thin paraffin embedded nerve cross sections and stained them with anti-neurofilament-antibody. Such staining (green fluorescence) revealed that pig infraorbital nerve is organized in 50–70 nerve fiber bundles (i.e., 54, 55, and 63 bundles in the three nerves studied; Figure 3(b)), not unlike the organization of the rat infraorbital nerve (Jacquin et al., 1984). High-resolution epifluorescence images of anti-neurofilament-antibody stained fiber bundles were then used to count nerve fiber numbers (Figure 3(c)). To also assess the myelination of the pig infraorbital nerve, we stained sections with luxol fast-blue and visualized myelin sheaths (Figure 3(d)). We performed fiber counts of five (of the 54) fiber bundles of the left infraorbital nerve of an adult pig (Figure 3(e)). Counts correlated well with the cross-sectional area of the fiber bundle and based on the total cross-sectional area we estimate that this left pig infraorbital nerve contained ~81,000 axons. In the same way, we arrived at an estimate of ~78,000 axons for the right infraorbital nerve. About 83% of these axons appear to be myelinated (Figure 3(f)). We conclude that pig rostrum is innervated by an impressive infraorbital nerve, which contains ~80,000 mainly myelinated axons.

3.3 | Nostril and rostrum skin folds match up with the blood sinus and folds of the rostrum gyrus

To appreciate the correspondence between periphery and cortical representation it is useful to picture the rostrum (photograph, Figure 4(a)) next to the rostrum gyrus. Accordingly, Figure 4(b) shows eight rostrum gyri. The gyri have been aligned to match rostrum orientation according to the topography results of Craner and Ray (Figure 1(c)). The gyri have been photographed with the arachnoidea and the blood sinus intact and have all been depicted to appear as left-hemispheric gyri. The gyri are similar, but not entirely stereotyped. A drawing of the rostrum and the rostrum gyri are shown in Figure 4(c,d), respectively.

In these drawings, we offer an interpretation of gyral folds and sulcus and blood sinus in terms of rostrum skin fold and nostril. We argue that the representation of the pig nostril (blue, Figure 4(c))
FIGURE 5  Legend on next page.
coincides in all gyri as the major middle sulcus (blue, Figure 4(d)). This major middle sulcus is observed in all rostrum gyri. In addition, we suggest that the lateral upward curving rostrum skin fold (red, Figure 4(c)) coincides in all eight gyri as an upward curving blood sinus (red, Figure 4(d)). This blood sinus is also associated with a major cortical fold and a change in gyrus curvature. Eventually, we suggest that the representation of the middle horizontal rostrum skin fold between the nostrils (green, Figure 4(c)) coincides in most gyri (7 out of 8) with a more or less horizontal blood sinus (green, Figure 4(d)).

The suggested correspondence of cortical blood sinus with rostrum skin folds aligns well with the receptive field data (Figure 1) reported by Adrian (1943) and Craner and Ray (1991).

On all rostrum gyri, we observed that the medial blood sinus (red in Figure 4(d)) locates to Position 2 in Adrian's gyrus (Figure 1(b)). From the receptive field map (Figure 1(a)), the Position 2 was that of the major dorsolateral skin fold on the rostrum. The same correspondence was depicted by Craner and Ray (1991), who observed this blood sinus and their receptive fields (Positions 3 and 4; Figure 1(c,d)) also match up with the dorsolateral skin fold. These observations suggest a correspondence between rostrum nostril and skin folds on the one hand with cortical sulci, blood sinus and folds in the somatosensory cortex on the other hand.

A quantitative assessment of the geometrical correspondence of rostrum and rostrum gyrus is given in Figure 4(e–j). Accordingly, we superimposed drawings of eight hemi-rostra in Figure 4(e) after scaling them to the same dorsoventral height. The drawings of the different rostra superimpose rather precisely suggesting little interanimal variability. In Figure 4(f), we show a similar superposition of the blood vessel patterns around rostrum gyri, which have been scaled to the same longitudinal length (the axis along which the dorsoventral height is represented; Figure 1). It is obvious that the putative nostril in the rostrum gyrus is collapsed and that blood vessels superimpose also well, albeit not as precisely as rostra outlines. In the subsequent panels, we use the relative metrics to the left and the top of the drawings in Figure 4(e,f) to compare rostra and gyri. Thus, as shown in Figure 4(g) the lateral position of the nostril and the putative nostril representation in the gyrus are similar, but not the same. Likewise, the relative position of other features of the rostrum (Figure 4(h)) and rostrum gyrus (Figure 4(i)) correspond well. Moreover, the relative angle of the lateral rostrum fold and the relative angle of the corresponding gyral blood sinus are similar (Figure 4(j)). Equally striking as the overall similarity is the substantially larger variability of the rostrum gyri compared to rostra.

3.4 Geometrical correspondence of rostrum- and rostrum gyrus-sections

We prepared sections through the pig rostrum to better visualize the geometry of this complex structure. A vertical section through the rostrum centered on the left nostril is shown in Figure 5(a). Similarly, we sectioned the rostrum gyrus semiparasagittally (a topographically matching section plane according to Figure 1), as indicated in Figure 5(b). A side view of the lateral part of the rostrum reveals the internal geometry of rostrum and nostril (Figure 5(c)). It can be seen that nostril is not symmetrical and that dorsally a prominent ridge (middle arrow in Figure 5(c)) is observed, whereas the ventral part is more funnel-like. To reveal the geometry of the rostrum gyrus we prepared semiparasagittal sections and stained them for cytochrome oxidase reactivity, a stain, which reveals the metabolically highly active Layer 4 by a brownish precipitate (Figure 5(d)). Note that rostrum gyrus is also not symmetrical in anterior–posterior direction. The posterior part of the gyrus also shows a ridge (middle arrow in Figure 5(d)), whereas the anterior part is more funnel-like. The drawing in Figure 5(e) confirms the correspondence of semiparasagittal gyrals to vertical rostrum sections (arrows in Figure 5(c–e)).

Horizontal sections through the pig rostrum (Figure 5(f)) and coronal sections through the rostrum gyrus (Figure 5(g)) led to similar conclusions. The nostril is not straight, but oblique (Figure 5(h)) and is represented in an oblique sulcus apparent in coronal sections and stained for cytochrome oxidase reactivity (Figure 5(i)). The drawing in Figure 5(j) confirms the correspondence of coronal gyrals to horizontal rostrum sections (arrows in Figure 5(h–j)).

These observations show that the internal geometry of the rostrum gyrus reliably matches the internal geometry of the rostrum itself.

**FIGURE 5** Geometrical correspondence of rostrum and rostrum gyrus in orthogonal sections. (a) Frontal view photograph of a vertical rostrum section centered on the left nostril. (b) Top view photograph of a right-hemispheric rostrum gyrus with the semiparasagittal plane of section superimposed. (c) Photograph of the lateral part the rostrum from the side. Arrows mark putative sites of correspondence to the rostrum gyrus section shown in (d,e). A dashed line below the skin has been superimposed to highlight the skin curvature. (d) Micrograph of a semiparasagittal rostrum gyrus section stained for cytochrome oxidase reactivity. Arrows mark putative sites of correspondence to the rostrum gyrus section shown in (c). Scale bar and orientation arrows apply to both (d,e). (e) Drawing of the semiparasagittal rostrum gyrus section shown in (d); the strongly cytochrome oxidase reactive Layer 4 on the outer rostrum gyrus is highlighted by the brownish color. Arrows mark putative sites of correspondence to the rostrum gyrus section shown in (c). Scale bar and orientation arrows apply to both (d,e). (f) Frontal view photograph of a horizontal rostrum section centered on the right nostril. (g) Top view photograph of a left-hemispheric rostrum gyrus with the coronal plane of section superimposed. (h) Photograph of the dorsal part of the rostrum from below. Arrows mark putative sites of correspondence to the rostrum gyrus section shown in (i,j). A dashed line below the skin has been superimposed to highlight the skin curvature. (i) Micrograph of a coronal rostrum gyrus section stained for cytochrome oxidase reactivity. Arrows mark putative sites of correspondence to the rostrum gyrus section shown in (h). (j) Drawing of a semiparasagittal rostrum gyrus section shown in (i); the strongly cytochrome oxidase reactive Layer 4 on the outer rostrum gyrus is highlighted by the brownish color. Arrows mark putative sites of correspondence to the rostrum gyrus section shown in (h). Scale bar and orientation arrows apply to both (i,j). A = anterior; P = posterior; M = medial; L = lateral.
FIGURE 6  Legend on next page.
3.5 | Serial sections, a Layer 4 flat map neuron counts of the rostrum gyrus

Since the rostrum gyrus is a folded structure, its architecture cannot be fully appreciated without sectioning. We therefore prepared serial sections of the rostrum gyrus. The intact rostrum gyrus (after removal of the arachnoidea with superimposed sectioning pattern) is shown in Figure 6(a) along with a hemi-rostrum (Figure 6(b)). In Figure 6(c), we show drawings of coronal sections. We drew Layer 4, the pia and the white matter border from sections stained for cytochrome-oxidase activity as shown in Figure 5. The serial sections again reveal that the middle sulcus is not symmetrical but oblique running from lateral (deep) to medial (surface). Thus, the orientation of the sulcus matches with the oblique orientation of the pig nostril, which runs from medial (deep) to lateral (surface) in body topography. It is also obvious that Layer 4 becomes very thin deep in the sulcus.

Despite numerous attempts, we were unable to flatten rostrum gyri such that the Layer 4 was contained in one tangential section. We therefore generated a digitally flattened version of Layer 4 from our drawings of Layer 4 in serial sections. We show the resulting digitally generated Layer 4 flat map in Figure 6(d)), in which we coded the Layer 4 thickness by gray scale. The thinning of Layer 4 in the putative nostril representation can be appreciated. The extraordinary area of the unfolded rostrum gyrus is also obvious from this representation. Thus, this fine grain serial-section-analysis of the gyrus confirms the geometrical correspondence to the rostrum and the unfolding reveals the full extent of gyral surface area. We assessed the extent of the gyral Layer 4 surface area (as drawn in Figure 6(c)) in four hemispheres and found to be on average 274 mm² (229–312 mm²).

By using stereological techniques, we estimated the total number of neurons in the entire rostrum gyrus. The total number of neurons in the rostrum gyrus area is around 8.2 million (n = 2). For the first series with Nissl stained sections, we have a total number of 9.738,526 with a corresponding CE of 0.02 (Gundersen m = 1). For series of gyral sections stained with anti-NeuN antibodies, we estimated total number of 6.663,724 neurons with a corresponding CE of 0.04 (Gundersen m = 1). Note that both coefficients of errors are lower than 0.1, a value considered to be reliable by earlier studies (Eriksen & Pakkenberg, 2007).

3.6 | The laminar organization and cytoarchitectonics of the rostrum gyrus

To assess the laminar organization, we stained serial sections of the rostrum gyrus with a variety of staining protocols (Figure 7). In particular, we visualized neurons in the rostrum gyrus using the pan-neuronal antibody NeuN (green fluorescence, Figure 7(a)). In the same sections, we visualized thalamic afferent innervation using antibodies against vesicular Glutamate transporter-2 (red vGlut-2 fluorescence; Figure 7(a)). The surface parts of the rostrum gyrus showed a very thick middle layer of red vGlut-2 fluorescence, presumably the thalamic Layer 4 innervation, and such vGlut-2 fluorescence was more prominent in the rostrum gyrus than in any other cortical region investigated (Figure 8). In line with results from the cytochrome-c-oxidase reactivity in Figure 6, we found the layer of red vGlut-2 fluorescence to be thinner in the sulcus.

The idea of a very prominent Layer 4 in the surface parts of the rostrum gyrus was confirmed by staining for cytochrome-c-oxidase reactivity of same/adjacent section (Figure 7(b)). Cytochrome-c-oxidase reactivity has been found to be high in somatosensory cortex Layer 4 (Wong-Riley & Welt, 1980) and this appears to be the case also in the pig’s rostrum gyrus (Figure 7(b)). Specifically, we observed strong cytochrome-c-oxidase reactivity (revealed by a brownish precipitate) exactly, where we had observed strong vGlut-2-antibody fluorescence. We observed that blood vessel density was highest in Layer 4 of the rostrum gyrus. We also prepared Nissl stained sections of the rostrum gyrus (Figure 7(c)). We found that the rostrum gyrus has a distinct appearance in Nissl-stains: a very thin Layer 1, lacked a distinct Layer 2 and prominent Layer 5b, which stands out by its low cell density.

Our conclusions, on the laminar organization of the rostrum gyrus (an absence of distinct Layer 2, a prominent Layer 4, a noncell dense Layer 5) are also captured in the drawing shown in Figure 7(d) and a high-magnification synopsis of staining patterns is shown in Figure 7(e).

We prepared Golgi stains of coronal sections of the rostrum gyrus to obtain insights in the cellular morphology of this brain region. A micrograph of a Golgi-stained section is shown in Figure 7(f). We then derived drawings of neuronal morphologies across the cortical column (Figure 7(g)); we restricted such drawings to spiny putatively excitatory neurons. As a result of sectioning and incomplete staining, such drawings reveal only partial morphologies. Still, Golgi staining revealed classic cortical morphologies of large Layer 3 and 5 pyramids and fusiform cells in the deepest and most superficial cortical layers. Layer 4 neurons of the rostrum gyrus stood out by nonpyramidal morphologies, very small somata and thin and short dendrites (Figure 7(h)).

How different is the rostrum gyrus from the rest of somatosensory cortex? This question is addressed in Figure 8, where we show cytoarchitectonic samples from different parts of pig somatosensory cortex (Figure 8(a)). It is apparent that the rostrum gyrus is characterized by a particularly thin Layer 1 (Figure 8(b,c)) and dense innervation by thalamic afferents (recognized by the vGlut-2-antibody; Figure 8(d)).

FIGURE 6 | Coronal sectioning and Layer 4 flat map of the rostrum gyrus. (a) Photographs of the right-hemispheric rostrum gyrus. The superimposed lines indicate positions of the subsequent sectioning. (b) Drawing of a hemi-rostrum. (c) Drawings of serial coronal sections through the rostrum gyrus. Drawings were made from sections stained for cytochrome-oxidase reactivity (see Figure 5). Layer 4 is indicated as a brown stripe. Sections are arranged in three columns from posterior (top, left) to anterior (bottom right). (d) Digitally generated flat map of the rostrum gyrus. The thickness of Layer 4 was measured from the serial section shown in (c) and coded in gray levels. Each row represents a digitally flattened coronal section (30 in total). Because we kept only every sixth section adjacent sections show slight discontinuities. To resolve this, we filled up this “empty space” by interpolating the Layer 4 thickness data in the anterior–posterior direction yielding a map with 180 rows.
FIGURE 7  Legend on next page.
(c). The marked thalamic innervation of the rostrum gyrus might also be reflected in the strong Layer 4 cytochrome-oxidase reactivity in the rostrum gyrus (Figure 8(d)).

Collectively, these data suggest a specialized laminar architecture of the rostrum gyrus.

3.7 | The Layer 4 of the rostrum gyrus is parvocellular, but not cell-dense

Given our results from the vGlut-2-antibody fluorescence and the cytochrome-c-oxidase reactivity we expected to see a prominent Layer 4 also in Nissl stains. This was not the case, however, and we consistently observed a lack of distinct “cell-dense” Layer 4 in Nissl stains (Figure 7(c)). We therefore investigated this issue more closely in our NeuN/vGlut2 antibody stained sections (Figure 9). The analysis of these staining patterns led to the same conclusion. Layer 4 is parvocellular (Figure 9(a,b)), but not cell-dense in the pig rostrum gyrus; instead it has a lower cell density than Layer 3 (Figure 9(c–f)).

There was also scattered evidence for the presence of weakly delineated barrels in Layer 4 of the rostrum gyrus. Such modules could be visualized in both coronal sections and in tangential sections of flattened gyri. Like rat/mouse whisker barrels they were visible as (dark) spots of heightened cytochrome oxidase reactivity on the background of lighter “septa.” When visible, barrels were elongated, rather round and had an average area of 0.067 ± 0.021 mm² (mean ± SD; 69 barrels from three different brains) in tangential sections. These structures may be rostrum gyrus barrels, corresponding to the aforementioned rostrum microvibrissae, an interpretation to be taken with caution for the following reasons: (a) the barrels were always only barely visible; (b) barrels could not be seen in all preparations; and (c) we have no corroborating electrophysiological evidence for microvibrissae responses in these structures.

These data show that Layer 4 of the rostrum gyrus is unusually thick, consists of small cells and is not cell-dense.

3.8 | Isomorphism of rostrum and rostrum gyrus

The gist of our anatomical observations is summarized in two drawings of rostrum and rostrum gyrus in Figure 10. The isomorphism is readily apparent in oblique lateral view of the rostrum and a mediadorsal view of the rostrum gyrus. Such striking isomorphism was also evident in photographs of rostrum gyrus and rostrum (not shown). Viewed this way the rostrum gyrus appears to be a ~1:2 sized model of the rostrum. As laid out throughout the article, the rostrum gyrus mimics folds, internal structure, surface curvature, and proportions of the rostrum. Alignment and removal of color information by the drawing capture how much the cortex actually morphs into a rostrum. We suggest this visualization reveals a trick of the brain, that is, the isomorphic arrangement of somatosensory cortical neurons.

4 | DISCUSSION

4.1 | Summary

The pig’s rostrum is an elaborate organ with a specialized integument and 900 microvibrissae and characteristic skin folds. We find that blood sinus, folds, and the middle sulcus of the rostrum gyrus correspond to the rostrum’s skin folds and nostril. Sectioning reveals the rostrum gyrus mirrors also the internal geometry and shape of the rostrum. The rostrum gyrus has specialized laminar architecture with a very thin Layer 1, an indistinct Layer 2 and noncell dense Layer 5. Layer 4 is very thick, not cell-dense (i.e., indistinct in Nissl stains) and made of very small cells. The rostrum gyrus appears as a three-dimensional (3D) model of the rostrum at a scale of ~1:2.

4.2 | The pig rostrum

Our data show that the pig rostrum has a highly stereotyped layout. In particular, we find that the rostrum has a number of skin folds that are very similar from animal to animal. Our micro-CT scans also confirmed earlier observations on the rich and diverse musculature of the pig rostrum (Herring, 1972). These muscles presumably underlie the extraordinary motility of the pig rostrum.

What has perhaps been less obvious in previous research is the prominence of microvibrissae in the pig rostrum. When we think of vibrissal sensing, we typically think of rats or mice, and few
FIGURE 8  Legend on next page.
investigators are aware that pigs have more vibrissae on their rostrum than rats or mice have on their entire body. The dense spacing of microvibrissae on the rostrum skin and the dense packing of follicles/microvibrissae blood sinus in our micro-CT scans of the rostrum inside is a very significant finding in our view.

Given the behavioral significance, it is not surprising that the pig infraorbital nerve that innervates the rostrum is very prominent. The pig infraorbital nerve shows a similar organization in numerous bundles as the rat infraorbital nerve (Jacquin et al., 1984). Somewhat surprisingly, our ~80,000 estimate of the number of axons in the pig infraorbital nerve is only ~2.5 x the number of axons reported for the rat infraorbital nerve (i.e., 33,059; Jacquin et al., 1984). Given the much larger body weight of pigs and the large diameter of the pig infraorbital nerve compared to rats, we would have expected a larger difference in peripheral innervation.

4.3 | Isomorphic representation

An isomorphic representation of the periphery has been observed in numerous somatosensory cortices. The key study for the recognition of an anatomical isomorphism between cortex and periphery was unquestionably Woolsey and Van der Loos’s (1970) study on the barrel cortex and whisker pad. Woolsey et al. subsequently showed that such a barrel-whisker isomorphic representation is common to many mammals (Rice, 1995; Woolsey et al., 1975). A striking isomorphism of cortical anatomy and periphery has been described in the star-nosed mole (Catania & Kaas, 1995). While strongly isomorphic representations have been mainly described in small brains, they are certainly not restricted to small brains. In particular, the discovery of “finger-isomorphs” in the somatosensory cortex of primates (Jain et al., 1998; Qi & Kaas, 2004) shows that large-scale isomorphic representations exist. The work of Welker on the raccoon forepaw representation also pointed in this direction (Welker, 1990; Welker & Seidenstein, 1959).

A different, albeit related, example of a close relationship of body and cortical representation was described by Adams and Horton (2002) for the visual cortex. As detailed by Adams and Horton (2002) the retinal blood vessel pattern leads to “angioscotomas,” which are precisely reflected in maps of metabolic activity (cytochrome oxidase reactivity) in visual cortex.

4.4 | A 3D 1:2 model of the rostrum in the rostrum gyrus

While the topographic representation of the body in “somatosensory cortical maps” is common knowledge, the intricate 3D representation of the rostrum in the pig rostrum gyrus comes as news. Is the 3D-model, we claim to observe real or could our observations come about accidentally as a byproduct of conventional two-dimensional cortical map? We think it is highly unlikely that the numerous 3D features of the rostrum gyrus (surface curvature, ridges, folds, oblique sulci) could come about by chance and then magically match with the rostrum geometry. While we claim that there is a 3D model of the rostrum, we do not claim that somatosensory cortex forms an entire 3D model of the pig’s body. Instead, we suggest that cortical architecture is modular and that the rostrum—a body part of immense sensory relevance for the pig—is represented in a separate 3D module. We also do not expect 3D brain-body-isomorphism in small-brained mammals. Cortical gyriﬁcation depends in a nonlinear fashion on cortical surface area. In mammals with a cortical surface area ≤10 cm², there are no gyri and the cortex is obligatory organized as a two-dimensional sheet (Hofman, 1985; Striedter et al., 2015). Thus, in small-brained mammals, there is an obligatory organization of the somatosensory cortex as a two-dimensional map. We suggest looking for other 3D body-part models in the somatosensory cortex of large-brained highly tactile mammals.

4.5 | Isomorphic cortical computation

The computational signiﬁcance of isomorphic cortical representations is a still unfathomed issue (Brecht et al., 2013). A key advantage of isomorphic representations might be the precise translation of neighborhood relationships into neural space. We suggest that such advantages—which have been widely recognized for two-dimensional cortical maps—also extend into the third dimension.

We have argued earlier that the simulation of bodily experience is a key functionality of somatosensory cortex (Brecht, 2017). In particular, we have pointed out that simulation of tactile experience rather than the transformation and elaboration of tactile response properties in a Hubel and Wiesel-like scheme might be key to understanding somatosensory cortex. The faithful 3D model of the rostrum in the rostrum gyrus lends itself as a substrate of such body simulation.

**FIGURE 8** Cytoarchitectonics of the rostrum gyrus and various other somatosensory cortical regions. (a) Right cortical hemisphere of a pig. Thick black lines indicate the plane of sections from various somatosensory cortical regions (identified according to the maps of Craner and Ray (1991). (b) Nissl stained coronal sections from various somatosensory cortical regions. Note the thin Layer 1 and the absent Layer 2 in the rostrum gyrus. (c) Coronal sections from various somatosensory cortical regions double-stained with anti-NeuN-antibodies (green, revealing neuronal somata) and anti-vesicular glutamate transporter-2 (vglut-2 red, revealing thalamic afferents). Note the marked red vglut-2 signal in Layer 4 of the rostrum gyrus, revealing intense thalamic innervation. (d) Coronal sections from various somatosensory cortical regions histochemically stained for cytochrome-c-oxidase reactivity. Note the intense cytochrome-c-oxidase reactivity in Layer 4 of the rostrum gyrus. All images within (c) have been acquired with the same camera settings. All micrographs were clipped above the pia (top of the micrographs) and around the Layer 6/white matter border (bottom of the micrographs). S1 = primary somatosensory cortex; A = anterior; V = ventral; L = layer. The bottom right scale bar applies to all panels in (b–d)
FIGURE 9 Legend on next page.
We argue that isomorphic representation is key feature of cortical architecture. As pointed out by Welker (1990), brainstem and spinal cord circuits look structurally much more similar across mammals than the cerebral cortex. This observation suggests that brainstem and spinal circuits do not mimic the distinct bodies of the various mammals. In contrast, the cerebral cortex has a highly species-specific appearance and in case of the somatosensory cortex such species-specific molding of the cortical sheet apparently can take the shape of a 3D model. It is worth pointing out that the default layout of the somatosensory cortex is that of a simple two-dimensional sheet. What comes closest to the 3D rostrum model observed in the rostrum gyrus is perhaps the gyral patterning of the raccoon forepaw somatosensory cortex as described by Welker and Seidenstein (1959). Here, sulci divide forepaw fingers. Thus, the raccoon somatosensory cortical forepaw representation looks like a forepaw model. Both the pig (see below) and the raccoon are extreme tactile specialists. Hence, we suggest that the two-dimensional sheet of the somatosensory cortex can be transformed into a 3D model if the system is under very strong selective pressure as it is the case in tactile specialists.

**4.6 Alignment of cortical blood sinus to rostrum features**

Our analysis clearly showed cortical blood sinus align with the representation of rostrum features. Since we do not think that these vessels perform computations, we wonder how this correspondence is to be explained. One possibility is that an alignment of cortical blood vessels and cortical representation is coincidental and simple byproduct of cortical folding (which in turn mimics rostrum folds). Alternatively, there might be a deeper functional connection. For example, it has been shown that cortical vascularization can affect cortical development and neuronal migration via the reelin-signaling system (Bethani et al., 2018).

**4.7 Tactile specialization of the pig brain**

The pig brain is clearly highly specialized for rostrum touch. The cortical surface area of the rostrum gyrus is huge (274 mm²), roughly 20 times that of the monkey finger area (~12 mm²; Nelson et al., 1980); the relative size of the pig rostrum gyrus compares to other tactile specialists, that is, the rat macrovibrissae representation in barrel cortex. It appears that pig tactile specialization has more marked consequences in the pig's cortex than in the peripheral innervation. Specifically, rat infraorbital nerve (Jacquin et al., 1984) and pig infraorbital nerve (which innervate vibrissae and rostrum, respectively) are less different in neuron number (only a factor of 2–2.5) than rat macrovibrissae cortex (Meyer et al., 2013) and pig rostrum cortex (which differ almost 20-fold in neuron number). Note, however, that our cortical cell counts are based on only two specimens; further and more detailed work along the lines of the barrel cortex study by Meyer et al. (2013) is needed to fully assess rostrum gyrus neuron numbers.

While primate touch and finger somatosensory cortex has been studied in hundreds of publications, however, we still know very little about the pig's tactile abilities. The sheer size of the rostrum cortex suggests that we could learn a lot from studying pig rooting behavior and touch. A study of the development of the rostrum gyrus might tell us how cortical 3D models of body parts are created. The rostrum is of immense behavioral significance to pigs. Specifically, pigs engage in rooting behavior and constantly keep their nose engaged (Graves, 1984). When pigs are abundant, rooting behavior has a major ecological impact on soil structure and this is how pigs can have detrimental effects as an invasive species (Sweitzer & Van Vuren, 2002).

The nostril representation in the pig rostrum gyrus shows remarkable similarities to the somatosensory nose cortex of rodents.
(Maier et al., 2020). The pig’s somatosensory cortical nostril representation is characterized by a thin Layer 4, much like we observed it in rat somatosensory nose cortex. Interestingly, we observed a strong locking of neural activity to respiration in rat nose cortex and we wonder if in pigs the rostrum cortex will also interact with respiratory and olfactory processing. One would imagine such nose-cortex smell interactions will be useful in the rostrum gyrus of pigs the rostrum cortex will also interact with respiratory and olfactory processing. One would imagine such nose-cortex smell interactions will be

4.8 Conclusion

We found that the pig rostrum gyrus has the shape of a 3D model of the rostrum. Further work is needed to understand the functional implications of this cortical body part model. Comparative studies should explore if this 3D cortical isomorphism is unique to pigs or if more large-scale body part models are hidden in cortical sulci and gyri of other species.

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AUTHOR CONTRIBUTIONS

All authors had full access to all the data in the study and take responsibility for the integrity of the data and the accuracy of the data analysis. Cindy Ritter, Eduard Maier, and Michael Brecht: Study concept and design. Cindy Ritter, Eduard Maier, Undine Schneeweiß, Tanja Wölk, Jean Simonnet, Lennart Eigen, Elcin Tunckol, and Leopold Purkart: Acquisition of data. Cindy Ritter, Eduard Maier, Safaa Malikawi, and Michael Brecht: Analysis and interpretation of data. Cindy Ritter and Michael Brecht: Drafting of the manuscript. Cindy Ritter and Michael Brecht: Statistical analysis. Michael Brecht: Obtained funding. Michael Brecht: Administrative, technical, and material support. Michael Brecht: Study supervision.

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DATA AVAILABILITY STATEMENT

We share all data and images published in this article.

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