9 The Cognitive Neuroanatomy of Human Ventral Occipitotemporal Cortex

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ABSTRACT Variability in human brain structure and function contributes to variability in perception and cognition. Nevertheless, in addition to the structural-functional variability of human ventral occipitotemporal cortex (VOTC), recent research reveals an unprecedented correspondence among cortical folding, functional representations, cytoarchitectonic areas, and white matter tracts in VOTC. This organization is remarkably stable across individuals and has been causally linked to domain-specific aspects of perception. In this chapter we provide a comprehensive review of this growing body of work. We use VOTC as a model system because it (1) plays an integral role in high-level visual perception and (2) displays an elegant correspondence between structure and function across spatial scales—from cells to networks. Specifically, we highlight that the correspondence between the anatomical and functional organization of VOTC can be used to (1) motivate and test computational models, (2) understand how neural responses in VOTC change during different cognitive tasks, and (3) relate to the perception of specific stimulus categories. Together, the findings reviewed in the present chapter lay the foundation for a new subdiscipline of cognitive neuroscience, which we refer to as *cognitive neuroanatomy* (CNA). We formally define CNA and end this chapter by proposing future applications of CNA.

A central question in cognitive neuroscience asks *How is the anatomy of the human brain linked to computations underlying neural responses and perception?* Let us consider the complexity of this question with one anatomical feature—cortical folding. Neuroanatomists write extensively about the "bewildering diversity" (Bailey & von Bonin, 1951) of cortical folding and how this variability or "diversity" corresponds to individual differences in cognition (Van Essen & Dierker, 2007). This variability extends to additional anatomical features across spatial scales—from microns to centimeters—which then add further complexity to understanding correspondences among brain structure, brain function, and perception. Contemporarily, Van Essen and Dierker (2007) state that "individual variability of the human cerebral cortex is a source of both fascination and frustration. The fascination arises because variability in cortical structure and function may account for many aspects of our unique personalities and cognitive capabilities. For neuroimagers, the frustration arises because variability presents serious obstacles when attempting to assign particular functional activation patterns to specific cortical areas" (p. 1050).

However, despite variability in brain structure, brain function, and perceptual abilities among individuals, recent evidence indicates that there are also stable features in brain structure across spatial scales and consistencies in the structural-functional coupling of cortical systems from one person to the next—especially within *human ventral occipitotemporal cortex* (VOTC)—that are perceptually meaningful. As such, the two main goals of this chapter are to (1) provide a comprehensive review of this stability and the orderliness it produces within human VOTC and (2) explain how this orderliness is not epiphenomenal. Indeed, as this section of the book is dedicated to perception and cognition, VOTC is an ideal model system to show how an understanding among cortical microstructure, cortical macrostructure, and white matter connectivity informs computational models that leverage this anatomical knowledge to provide insights into the underpinnings of high-level perception (e.g., word and face recognition).

In line with these goals, this chapter is divided into four sections. First, we review studies demonstrating a strong anatomical-functional coupling between cortical folding and functional representations spanning large-scale functional gradients and fine-scale functional regions within VOTC. In the second and third sections, we discuss two anatomical constraints that contribute to this structural-functional coupling: cytoarchitecture (e.g., the size, shape, and organization of cells across the layers of the cortical ribbon) and long-range white matter tracts connecting cortical regions. We then discuss how the consistent structural-functional organization of human VOTC motivates a new class of

mechanistic models that leverages anatomical features to predict neural responses and perceptual functions. In the first three sections, we modify Van Essen and Dierker's (2007) forms of variability to consistency. We consider *functional representation-versus-folding consistency*, *cytoarchitectonic area-versus-folding consistency*, *cytoarchitectonic area-versus-functional region consistency*, and *connectional-versus-folding consistency*. In the fourth section, we propose that the ability to build mechanistic models that relate microanatomical features to macroanatomical (and functional) structures contributing to perception is the foundation of an emerging new subdiscipline of cognitive neuroscience: cognitive neuroanatomy (CNA). We formally define CNA and describe how it complements other subdisciplines in cognitive neuroscience. We end by providing examples of new questions and applications that emerge from CNA.

Consistency of Cortical Folding and Functional Representations

The folding of the cortex consists of both gyri (e.g., ridges) and sulci (e.g., furrows) in which the latter encompass more surface area than the former in the human brain (Destrieux et al., 2010; Van Essen, 2005; Zilles et al, 1997). Consequently, since more surface area of the human brain is sulcal as opposed to gyral in nature, accurate sulcal definitions are imperative for (1) quantifying the correspondence between cortical folding and functional representations and (2) motivating novel insights into the neurobiological foundations of perception. For example, related to the latter point, a recent study showed a surprising link between the fractionation of the occipitotemporal sulcus (OTS) and reading skills (Cachia et al., 2018). In addition to the OTS, modern methods accurately identify deep sulci within human VOTC such as the calcarine and collateral (CoS) sulci. However, four shallower VOTC sulci are also consistently identified in individual hemispheres (figure 9.1*A*): (1) the mid-fusiform sulcus (MFS), which bisects the fusiform gyrus (FG) into lateral and medial partitions, (2) the anterior (ALS) and posterior lingual sulci (PLS), which separate the lingual gyrus (LG) into anterior, mid, and posterior components, and (3) the posterior transverse collateral sulcus (ptCoS), which is a transverse component of the CoS. As discussed in subsequent sections, these sulci are landmarks identifying functional representations in VOTC.

Functional representation-versus-folding consistency Recent studies show that the relationship between cortical folding and functional representations in VOTC is much tighter than previously thought. We consider two scales of this relationship: large-scale functional gradients that span approximately 5,000 mm^3 (Weiner et al., 2014) and fine-scale functional regions, which are approximately an order of magnitude smaller (~200–500 mm^3; Weiner and Grill-Spector, 2010; Weiner et al., 2018).

Large scale As previously described (Grill-Spector & Weiner, 2014), the MFS identifies transitions in many large-scale functional maps, or gradients, that are composed of continuous or discrete stimulus dimensions, such as eccentricity (Malach, Levy, & Hasson, 2002), semantics (Huth, Nishimoto, Vu, & Gallant, 2012), animacy (Haxby et al., 2011), real-world object size (Konkle & Oliva, 2012), domain selectivity (Nasr et al., 2011), and conceptual knowledge (Martin, 2007). Despite differences in functional content, each map shares a common spatial layout in which representations positioned lateral to the MFS are functionally distinct from those positioned medial to the MFS. For example, lateral to the MFS, representations are biased toward foveal signals, while medial to the MFS, representations are biased toward peripheral signals (Malach, Levy, & Hasson, 2002); this same gradient predicts responsiveness to large versus small objects (Konkle & Oliva, 2012). We emphasize that some of these large-scale, lateral-medial gradients are not limited to visual perception, as they are present in blind individuals (van den Hurk, Van Baelen, & Op de Beeck, 2017) and can be produced in VOTC when sighted individuals simply imagine stimuli (Konkle & Oliva, 2012). These findings boast an impressive amount of predictive power: simply identifying the MFS in a person's brain predicts transition points in multiple functional gradients.

Fine scale While the MFS is a useful landmark to identify transitions in large-scale functional gradients, recent evidence indicates that particular sulcal features are useful for identifying the location of fine-scale clusters in VOTC in three particular ways. First, high-resolution functional magnetic resonance imaging (fMRI) shows that the traditional fusiform face area is composed of two spatially distinct clusters separated by 1–1.5 cm. The anterior component (mFus-faces) colocalizes with the anterior tip of the MFS. In fact, placing a 1 cm disk at the anterior tip of the MFS predicts 83% ± 7% of mFus-faces in the right hemisphere across individuals (Weiner et al., 2014). Second, the intersection between the ALS and the occipital component of the CoS predicts the location of the parahippocampal place area (CoS-places). This sulcal intersection is such a consistent landmark that a model built from one

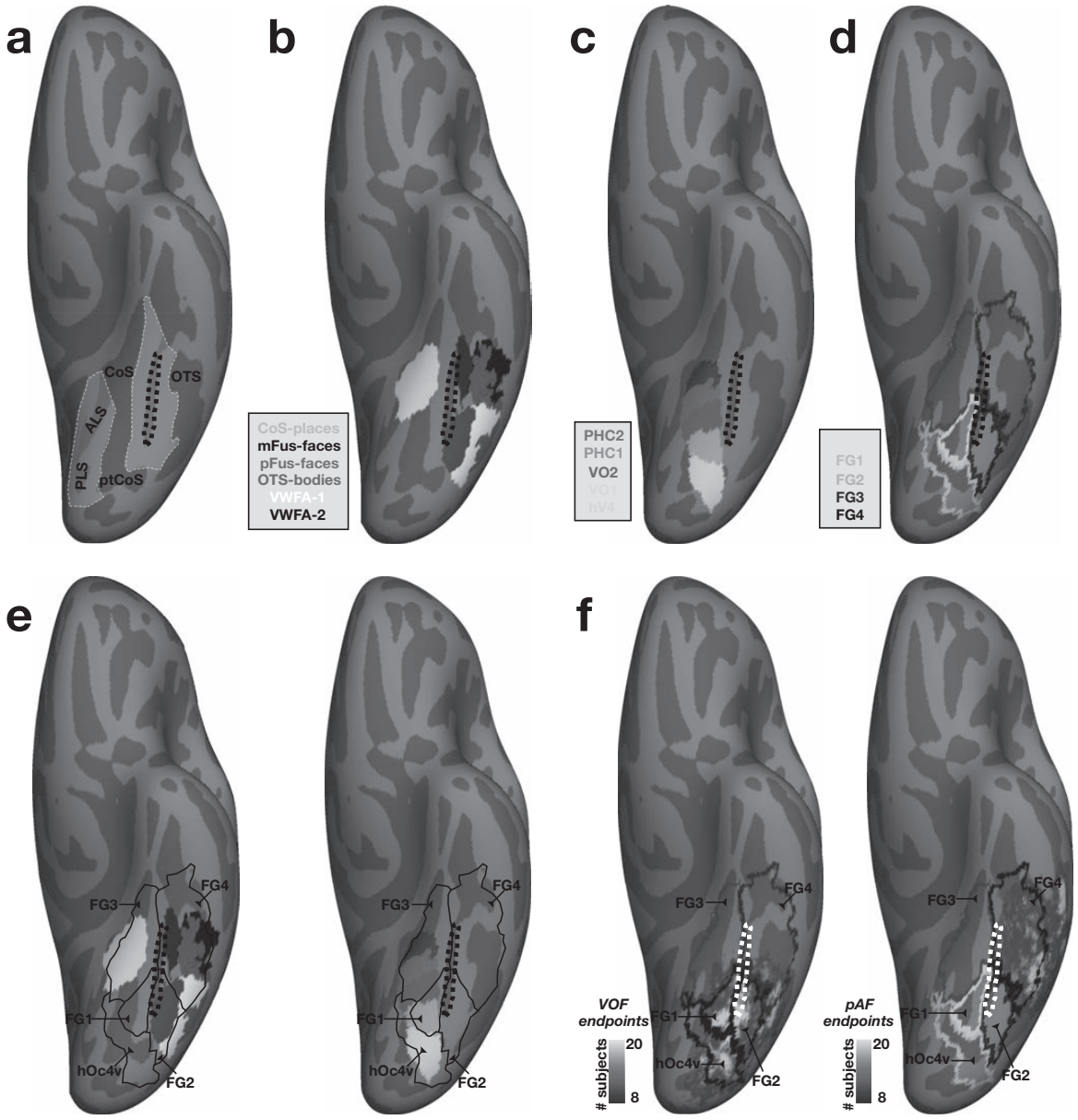

FIGURE 9.1 A correspondence among cortical folding, functional representations, cytoarchitectonic areas, and white matter endpoints in VOTC. Inflated left hemisphere of the FreeSurfer average template (www.freesurfer.net). *Dotted outline (black in A–E; white in F)*: Mid-fusiform sulcus. *A*, *Orange*: lingual gyrus; *blue*: fusiform gyrus; *ALS*: anterior lingual sulcus; *CoS*: collateral sulcus; *OTS*: occipitotemporal sulcus; *PLS*: posterior lingual sulcus; *ptCoS*: posterior transverse collateral sulcus. *B*, Maximum probability maps (MPMs) of domain-specific regions selective for faces, bodies, words, and places (see legend) from 12 individuals (Weiner et al., 2017). *C*, MPMs of retinotopic maps (see legend) defined from 53 individuals (Wang et al., 2015). *D*, MPMs of five cytoarchitectonic areas (see legend) defined from 10 individuals (Rosenke et al., 2018). *E*, Functional parcellations relative to cytoarchitectonic parcellations of VOTC. *Left*: domain-specific regions from (*B*). *Right*: retinotopic maps from (*C*). *F*, Probabilistic maps of cortical endpoints of the VOF (*left*) and pAF (*right*; $N = 37$; Weiner, Yeatman, & Wandell, 2017) relative to cytoarchitectonic areas from (*D*). (See color plate 11.)

group of participants can accurately predict the location of CoS-places in a separate group of participants (Weiner et al., 2018; figure 9.1*B*). Importantly, this structural-functional coupling between face- and place-selective regions and specific sulcal features is not epiphenomenal: electrical stimulation delivered to these locations produces domain-specific perceptual distortions (Megevand et al., 2014; Rangarajan et al., 2014). Third, the ptCoS identifies the boundary in the eccentricity maps distinguishing areas hV4 and VO-1 despite variability in cortical folding and map size (Witthoft et al., 2014; figure 9.1*C*). Of course, not all regions colocalize with sulcal features. In these cases, the topology of VOTC is useful. For example, body- and word-selective regions are consistently located lateral to face-selective regions within the OTS (Glezer & Riesenhuber, 2013; Weiner & Grill-Spector, 2010; Yeatman, Rauschecker, & Wandell, 2013).

The fact that there is functional representation-versus-folding consistency in VOTC is a major step forward for understanding the elegant correspondence between structure and function in high-level visual cortex. It also means that (1) anatomical axes reflect functional axes in VOTC and (2) fine-scale functional regions are embedded within large-scale functional gradients. Further, this nesting of functional representations is predicted by different scales of cortical folding: transitions in large-scale gradients are predicted by entire sulci, and local sulcal features predict the specific location of fine-scale functional regions.

Consistency of Cytoarchitectonics, Cortical Folding, and Functional Representations

Cytoarchitectonic area-versus-folding consistency Contrary to classic neuroanatomical studies, recent evidence supports a tight correspondence between sulci and cytoarchitectonic transitions in VOTC. Defined in the introduction, cytoarchitecture is considered the anatomical hardware that performs the computations underlying perception. Modern cytoarchitectonic approaches implement objective analyses in which algorithms traverse the cortical ribbon and statistically determine where adjacent pieces of tissue are cyotarchitectonically different (Amunts & Zilles, 2015). This algorithmic approach also allows the visualization of cytoarchitectonic areas using the same cortical surface-based methods that are used for visualizing in vivo MRI data. Employing these methods, eight areas have been identified in visual cortex, five of which are the most relevant for the present chapter: human occipital cytoarchitectonic area 4 ventral (hOc4v; Rottschy et al., 2007), as well as four cytoarchitectonic areas within the fusiform gyrus (FG1–FG4; Caspers et al., 2013; Lorenz et al., 2015; figures 9.1*D*, 9.2*A*). The MFS predicts cytoarchitectonic transitions between FG1 and FG2 in the posterior aspects of the FG, while the MFS also predicts cytoarchitectonic transitions between FG3 and FG4 in the middle portion of the FG. Additionally, the ptCoS predicts the transition between hOc4v and FG1 (Rosenke et al., 2018). Taken together, these findings also boast an impressive amount of predictive power: cellular-scale insight can be gleaned from centimeter-scale features of the cortical surface.

Cytoarchitectonic area-versus-functional region consistency In linking the previous two sections together, recent studies leveraged the fact that cytoarchitectonic areas and functional regions have a tight correspondence relative to cortical folding by developing tools to accurately project functional regions identified in living brains to cytoarchitectonic areas identified in post-mortem tissue (and vice versa). These studies (Rosenke et al., 2018; Weiner et al., 2017) produced three main discoveries. First, each functional region is largely restricted to one cytoarchitectonic area. For instance, hV4 is largely restricted to hOc4v, while mFus-faces is located in a different cytoarchitectonic territory in FG4 (figure 9.1*E*). Second, regions selective for the same domain (e.g., faces) and located on the same macroanatomical structure (e.g., the FG), can be differentiated based on cytoarchitectonics. For example, mFus-faces is located within FG4 and displays different cytoarchitectonic features than pFus-faces, which is located in FG2. Third, and contrary to classic theories (Brodmann, 1909), there is not a one-to-one correspondence between a cytoarchitectonic area and a functional region. For example, face-, body-, and word-selective regions are all clustered within FG4. Understanding how computational and perceptual insight can be gleaned from the cytoarchitecture of a functional region (figure 9.2*A*) is discussed in the final section of this chapter.

Consistency of Connections in Ventral Occipitotemporal Cortex: From Models of Anatomy to Models of Neural Computations

Connectional-versus-folding consistency As the MFS is a functional and cytoarchitectonic landmark in VOTC, we briefly summarize recent findings showing that white matter tracts also have a consistent relationship relative to the MFS. Specifically, using a face-selective region and a place-selective region as separate seeds, Gomez et al. (2015) identified two longitudinal white

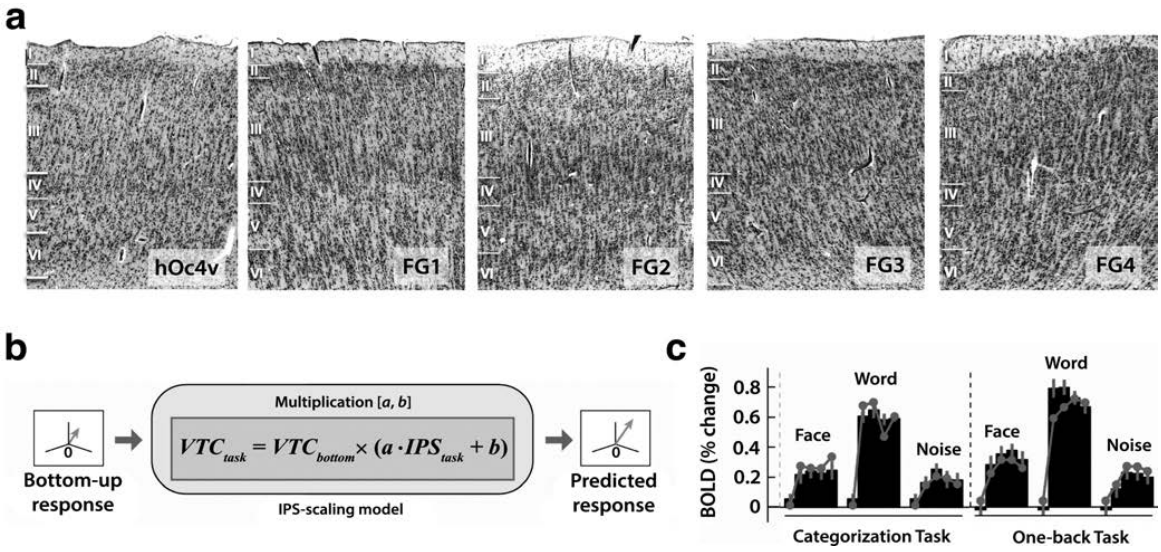

FIGURE 9.2 From cytoarchitecture to computational model architecture. *A*, Example histological slice from the five cytoarchitectonic areas in VOTC in figure 9.1 (modified from Rosenke et al., 2018). *B*, Architecture of the IPS-scaling model implemented by Kay and Yeatman (2017). The model begins with estimates of bottom-up neural signals in response to a stimulus (*left*). A top-down component is then added in which signals from the IPS modulate the neural responses within VWFA-1 using two free parameters (*middle*) to generate predicted responses, which are then compared to the actual measured responses (*right*). *C*, Blood oxygen level-dependent (BOLD) responses as a function of task (categorization; one-back) and stimulus (face, word, noise) during a contrast manipulation within VWFA-1. *Black bars*: measured BOLD responses; *gray lines*: model fits. There was a close correspondence between the model fits and the data (r = .96). As VWFA-1 is located within cytoarchitectonic area FG2, insights can now be made regarding how to incorporate cytoarchitectonic information into the model (see text for details).

matter tracts that were located (1) below the inferior longitudinal fasciculus and (2) lateral or medial to the MFS, respectively. Interestingly, the large-scale topology of these tracts was similar in typical adults and adults with prosopagnosia, or an inability to recognize faces. However, white matter properties within the tracts lateral, but not medial, to the MFS that intersected with face-selective regions were different between the patients compared to controls, indicating an important relationship between white matter properties and perception. Additionally, the endpoints of two vertical white matter tracts in VOTC, the vertical occipital fasciculus (VOF) and the posterior arcuate fasciculus (pAF), are also reliably positioned relative to the MFS: the anterior boundary of the VOF and the posterior boundary of the pAF are located near the midpoint of the MFS (figure 9.1*F*; Weiner et al., 2017; Yeatman et al., 2014). We emphasize that the cortical locations in which white matter tracts (1) start and end, as well as which (2) intersect with functional regions, guide both studies of perception and the construction of neurobiologically plausible computational models, which we expand on further below.

A tight correspondence among cortical folding, functional representations, cytoarchitectonic areas, and white matter endpoints in VOTC Because there is (1) a consistent relationship between white matter endpoints and cortical folding and (2) a consistent relationship between functional regions and cortical folding, it is perhaps intuitive to the reader that white matter terminations in VOTC colocalize with functional regions. Indeed, the correspondence between functional responses and white matter anatomy in VOTC is so strong that a model of an individual's white matter connections can predict (1) the location of functional regions in adults (Saygin et al., 2012) and (2) where functional regions will emerge over the course of development (Saygin et al., 2016). A series of recent studies also show that category-selective regions—such as pFus-faces and the first visual word form area (VWFA-1)—are situated within the ventral terminations of the VOF (Kay & Yeatman, 2017; Yeatman, Rauschecker, & Wandell, 2013). As described in the previous section, both functional regions are also located within cytoarchitectonic area FG2. By visualizing probabilistic maps of white matter endpoints (Weiner, Yeatman, & Wandell, 2017) relative

—-1
—0
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to probabilistic maps of cytoarchitectonic areas (Weiner et al., 2017), we can draw additional insights relating white matter transitions to cytoarchitectonic transitions (figure 9.1*F*). For example, VOF endpoints are largely restricted to FG1, FG2, and hOc4v. pAF endpoints are largely restricted to FG4. This suggests that there may be a relationship between large-scale white matter tracts and cytoarchitectonic boundaries, which can be examined further in future research. Taken together, there is a tight correspondence among cortical folding, functional representations, cytoarchitectonic transitions, and white matter endpoints in VOTC. We next illustrate how this precise anatomical knowledge can serve as the foundation for constraining models of cortical computation.

From models of anatomy to models of neural computations There are a wealth of studies in animals and humans in which knowledge of anatomical connections generates novel hypotheses about function—or lends support to a specific interpretation of information flow within a circuit (Noudoost & Moore, 2011; Saalmann, Pinsk, Wang, Li, & Kastner, 2012; and many others). Recently, anatomical connectivity was formally incorporated into a model of cortical computation within human VOTC (figure 9.2*B*), which linked task-driven modulations of word- and face-selective responses to the difficulty human observers experience when recognizing noisy images of words and faces (Kay & Yeatman, 2017). When attention is averted, the model showed that bottom-up response properties of pFus-faces and VWFA-1 could be computed by comparing a simple, V1-like representation of visual stimuli to a template of the preferred category. However, when viewers were prompted to make perceptual judgments of visual stimuli—such as categorizing an image as a word or a face—responses in category-selective regions were amplified by as much as 400%. This task-driven modulation of VOTC could not be explained by a bottom-up visual encoding model that simply predicted neural responses as a function of image features. However, when the authors considered that the VOF connected pFus-faces and VWFA-1 ventrally to regions of the intraparietal sulcus (IPS) that are involved in visual attention and perceptual decision-making, an intriguing question emerged: Could the observed, task-dependent modulation of VOTC responses reflect top-down signals that are related to the decision-making process within the IPS? Based on these anatomical connections, model modifications were made in which the IPS responses directly modulated the VOTC responses via signals conducted through the VOF. This top-down modulation introduced a gain to the bottom-up VOTC responses. This anatomically motivated model accurately predicted how responses in pFus-faces and VWFA-1 changed when the stimulus was held constant but the perceptual task changed (figure 9.2*B*). These results pave the way for new models that incorporate anatomical knowledge to predict how regions in human VOTC flexibly adapt to the demands of various perceptual tasks. For example, this model could serve as a general model explaining how top-down signals modulate visual encoding, which can be tested with additional perceptual tasks in future studies.

The Emergence of Cognitive Neuroanatomy

We have discussed how novel methodologies have generated insights into structural-functional correspondences in VOTC spanning spatial scales from cells to networks to computations underlying specific perceptual tasks. In this section we propose that these findings lay the groundwork for a new subdiscipline of cognitive neuroscience, cognitive neuroanatomy (CNA). In the sections below, we (1) provide a formal definition of CNA and (2) propose future applications of CNA based on the approaches reviewed in this chapter.

A formal definition of cognitive neuroanatomy CNA aims to explain how microanatomical structures generate macroanatomical functions contributing to measurable behaviors. At the heart of CNA is the goal to derive linking functions (e.g., models) that relate (1) behavioral output to (2) functional organization of the brain across spatial scales to (3) anatomical organization across spatial scales. The benefit of such functions is that once they are derived, specific aspects of human behavior can be explained as emergent properties of microarchitecture, macroarchitecture, and connectivity. As traditional anatomical measurements are made in static postmortem tissue, additional benefits are that once these linking functions are derived, variations in microanatomical features could predict variations in human behavioral performance. While this might seem far-fetched—for example, to predict behavioral performance in perceptual tasks from cellular or receptor measurements in postmortem tissue—in the next subsection, we show that this goal is not as far-fetched as it may seem.

Before doing so, we would like to clarify that *cognitive neuroanatomy* is a phrase that has appeared in the literature (Friston et al., 1996; Jäncke, 2003; Witelson, 1992) but without formal definition. The phrase was used interchangeably with *functional neuroanatomy*, *functional anatomy*, and *cognitive anatomy* (Friston & Price, 2003; Mechelli, Gorno-Tempini, & Price, 2003; Price &

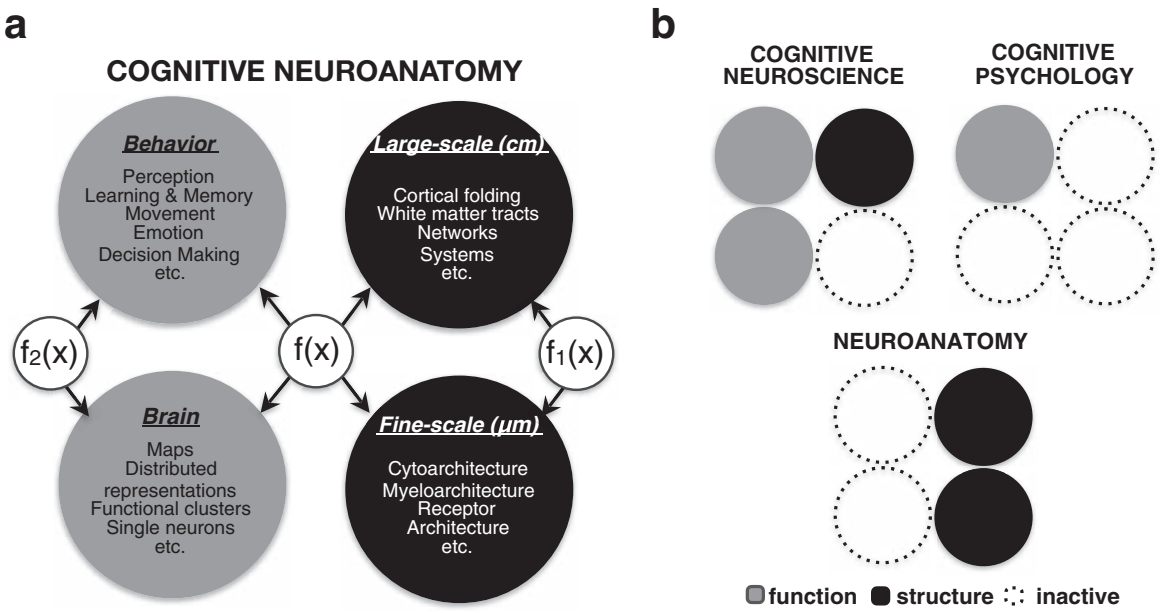

FIGURE 9.3 Cognitive neuroanatomy (CNA): a new subdiscipline of cognitive neuroscience. *A*, CNA works toward building mechanistic models explaining how microanatomical structures (*lower right*) generate macroanatomical functions (*lower left* and *upper right*) contributing to measurable behaviors (*upper left*) with an emphasis on deriving specific linking functions (depicted as $f_y(x)$). *B*, CNA integrates (1) cognitive neuroscience, which combines behavior with functional and structural features of the brain (three quadrants), (2) cognitive psychology, which incorporates function and behavior, as well as modeling (one quadrant), and (3) traditional neuroanatomy, which examines structural features of the brain across spatial scales (two quadrants). *Gray*: function; *black*: structure; *dotted line*: inactive.

Friston, 2002; Swanson et al., 1991). We do not see it as a phrase that is interchangeable with these other terms. Instead, CNA is a distinct subdiscipline of cognitive neuroscience emerging from a detailed understanding of anatomical principles that form the foundation of human brain computation and cognition. Subdisciplines become necessary as integration across fields increases (Naselaris et al., 2018). CNA can be considered the integration, or intersection, of cognitive psychology, cognitive neuroscience, and neuroanatomy (figure 9.3).

Future implementations of CNA based on the findings reviewed in the present chapter The model described in the previous section is an example of a linking function derived to explain how vertical white matter connections between VOTC and IPS carry signals that modulate processing in VOTC to accommodate the demands of face and word perception in the presence of noise. Progress can be gained by incorporating additional neuroanatomical and functional details to this (and future) model(s). Each successive step provides a new linking function—and with it, new insights into the architecture of human perception. For example, let us consider that VWFA-1 and pFus-faces are (1) already included in the model, (2) embedded within foveally biased cortex, (3) connected to the IPS through the VOF, and (4) located within FG2, which has a higher cell density than FG1 (Caspers et al., 2013). A logical hypothesis resulting from these structural-functional correspondences is that an increase in cell density is necessary to support the higher fidelity of foveal compared to peripheral processing. Previous neuroanatomical findings in nonhuman primates support this hypothesis by demonstrating that (1) cell density is highest in visual cortex compared to the rest of the brain, and (2) foveal representations in early visual cortex have higher neuronal densities than peripheral representations (Collins, Airey, Young, Leitch, & Kaas, 2010). Consequently, cell density across cortical layers serves a functional purpose and could be formalized into a model based on cytoarchitectonic data—for example, to predict differences in response properties between (1) posterior VWFA-1 and more anterior VWFA-2 (figure 9.1) and (2) mFus-faces and pFus-faces (figure 9.1). A perceptual component to the

model could also be added by including psychophysical performance on different tasks related to word and face perception (e.g., discrimination versus recognition). With this model architecture, simulations titrating cell density could provide insight into how increased versus decreased cell density affects model performance in predicting neural responses, as well as behavioral performance on different perceptual tasks.

Additional components could also be integrated from models that already exist in the extended fields of neuroscience, cognitive science, and neuroanatomy. For example, there are powerful models that accurately predict (1) cortical folding across species (Tallinen, Chung, Biggins, & Mahadevan, 2014) and (2) the topological organization of maps in visual cortex (Kohonen, 1990). Incorporating mechanistic models of both folding and functional topography into the infrastructure described in figures 9.1 and 9.2 would provide a flexible model that could provide cellular insights into perception beyond the extensively studied regions of VOTC. Simulations could examine how the combination of cell density and area size influence perception. For instance, previous research indicates that (1) the surface area of functionally defined V1 predicts variability in conscious experience (Schwarzkopf, Song, & Rees, 2011), (2) a greater proportion of V1 is devoted to foveal compared to peripheral processing (Dougherty et al., 2003), and (3) there is an increased cell density devoted to foveal compared to peripheral processing. Thus, it is likely that there is a relationship among (1) cell density, (2) the surface area of eccentricity representations within V1, and (3) perception. Finally, cortical thickness and the surface area of functional regions would also be valuable anatomical factors to consider, as prior research shows that thin cortex with an enlarged surface area is linked to neural tuning and is perceptually advantageous (Song et al., 2015). Importantly, such models for visual perception may serve as the foundation for CNA models in other parts of the brain. As such, the details of brain anatomy, which are often considered tedious, will incrementally improve evolving CNA models that provide mathematical formulas defining the computations underlying the architecture of human perception and cognition.

Conclusion

Individual differences in the structure and function of VOTC have been described as "fascinating and frustrating" (Van Essen and Dierker, 2007) and linked to individual differences in perception and cognition. Nevertheless, in this chapter we have summarized a broad body of work that empirically supports the orderliness of VOTC to the point where (1) we know how cells are organized in multiple functionally defined regions and (2) computational models that are motivated by anatomical connectivity can accurately predict neural responses in relation to specific perceptual tasks. These findings are built on the systematic progress that has leveraged the centuries of work leading to the foundational knowledge of CNA, which is a new subdiscipline of cognitive neuroscience. While we have derived the definition of CNA from our field's understanding of VOTC, we look forward to applying this definition throughout the study of the brain in the years to come.

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REFERENCES

Allison, T., Puce, A., Spencer, D. D., & McCarthy, G. (1999). Electrophysiological studies of human face perception. I: Potentials generated in occipitotemporal cortex by face and non-face stimuli. *Cerebral Cortex, 9*(5), 415–430.

Amunts, K., & Zilles, K. (2015). Architectonic mapping of the human brain beyond Brodmann. *Neuron, 88*(6), 1086–1107.

Bailey, P., & von Bonin, G. (1951). *The isocortex of man*. Urbana: University of Illinois Press.

Brodmann, K. (1909). *Vergleichende Lokalisationslehre der Großhirnrinde in ihren Prinzipien dargestellt auf Grund des Zellbaues*. Leipzig: Johann Ambrosius Barth Verlag.

Cachia, A., Roell, M., Mangin, J. F., Sun, Z. Y., Jobert, A., Braga, L., Houde, O., Dehaene, S., & Borst, G. (2018). How interindividual differences in brain anatomy shape reading accuracy. *Brain Structure and Function, 223*(2), 701–712.

Caspers, J., Zilles, K., Eickhoff, S. B., Schleicher, A., Mohlberg, H., & Amunts, K. (2013). Cytoarchitectonical analysis and probabilistic mapping of two extrastriate areas of the human posterior fusiform gyrus. *Brain Structure and Function, 218*(2), 511–526.

Collins, C. E., Airey, D. C., Young, N. A., Leitch, D. B., & Kaas, J. H. (2010). Neuron densities vary across and within cortical areas in primates. *Proceedings of the National Academy of Sciences of the United States of America, 107*(36), 15927–15932.

Destrieux, C., Fischl, B., Dale, A., & Halgren, E. (2010). Automatic parcellation of human cortical gyri and sulci using standard anatomical nomenclature. *Neuroimage, 53*(1), 1–15.

Dougherty, R. F., Koch, V. M., Brewer, A. A., Fischer, B., Modersitzki, J., & Wandell, B. A. (2003). Visual field representations and locations of visual areas V1/2/3 in human visual cortex. *Journal of Visualized Experiments, 10*, 586–598.

Friston, K. J., & Price, C. J. (2003). Degeneracy and redundancy in cognitive anatomy. *Trends in Cognitive Sciences, 7*(4), 151–152.

Friston, K. J., Price, C. J., Fletcher, P., Moore, C., Frackowiak, R. S., & Dolan, R. J. (1996). The trouble with cognitive subtraction. *NeuroImage, 4*(2), 97–104.

Glezer, L. S., & Riesenhuber, M. (2013). Individual variability in location impacts orthographic selectivity in the "visual word form area." *Journal of Neuroscience, 33*(27), 11221–11226.

Gomez, J., Pestilli, F., Witthoft, N., Golarai, G., Liberman, A., Poltoratski, S., … Grill-Spector, K. (2015). Functionally defined white matter reveals segregated pathways in human ventral temporal cortex associated with category-specific processing. *Neuron, 85*(1), 216–227.

Grill-Spector, K., & Weiner, K. S. (2014). The functional architecture of the ventral temporal cortex and its role in categorization. *Nature Reviews Neuroscience, 15*(8), 536–548.

Haxby, J. V., Guntupalli, J. S., Connolly, A. C., Halchenko, Y. O., Conroy, B. R., Gobbini, M. I., … Ramadge, P. J. (2011). A common, high-dimensional model of the representational space in human ventral temporal cortex. *Neuron, 72*(2), 404–416.

Huth, A. G., Nishimoto, S., Vu, A. T., & Gallant, J. L. (2012). A continuous semantic space describes the representation of thousands of object and action categories across the human brain. *Neuron, 76*(6), 1210–1224.

Jäncke, L. (2003). Current methods for cognitive neuroanatomy. In K. Hugdahl (Ed.), *Experimental Methods in Neuropsychology* (pp. 197–222). Dordrecht, the Netherlands: Kluwer Academic.

Kay, K. N., & Yeatman, J. D. (2017). Bottom-up and top-down computations in word- and face-selective cortex. *eLife, 6,* e22341.

Kohonen, T. (1990). Cortical maps. *Nature, 346*(6279), 24.

Konkle, T., & Oliva, A. (2012). A real-world size organization of object responses in occipitotemporal cortex. *Neuron, 74*(6), 1114–1124.

Lorenz, S., Weiner, K. S., Caspers, J., Mohlberg, H., Schleicher, A., Bludau, S., … Amunts, K. (2015). Two new cytoarchitectonic areas on the human mid-fusiform gyrus. *Cerebral Cortex, 27*(1), 373–385.

Malach, R., Levy, I., & Hasson, U. (2002). The topography of high-order human object areas. *Trends in Cognitive Sciences, 6*(4), 176–184.

Mangin, J. F., Auzias, G., Coulon, O., Sun, Z. Y., Riviere, D., & Regis, J. (2015). Sulci as landmarks. In A. W. Toga (Ed.), *Brain Mapping: An Encyclopedic Reference* (pp. 45–52). New York: Academic Press.

Martin, A. (2007). The representation of object concepts in the brain. *Annual Review of Psychology, 58*, 25–45.

Mechelli, A., Gorno-Tempini, M. L., & Price, C. J. (2003). Neuroimaging studies of word and pseudoword reading: Consistencies, inconsistencies, and limitations. *Journal of Cognitive Neuroscience, 15*(2), 260–271.

Megevand, P., Groppe, D., Goldfinger, M. S., Hwang, S. T., Kingsley, P. B., Davidesko, I., & Mehta, A. D. (2014). Seeing scenes: Topographic visual hallucinations evoked by direct electrical stimulation of the parahippocampal place area. *Journal of Neuroscience, 34*(16), 5399–5405.

Naselaris, T., Bassett, D. S., Fletcher, A. K., Kording, K., Kriegeskorte, N., Nienborg, H., … Kay, K. (2018). Cognitive computational neuroscience: A new conference for an emerging discipline. *Trends in Cognitive Sciences, 22*(5), 365–367.

Nasr, S., Liu, N., Devaney, K. J., Yue, X., Rajimehr, R., Ungerleider, L. G., & Tootell, R. B. (2011). Scene-selective cortical regions in human and nonhuman primates. *Journal of Neuroscience, 31*(39), 13771–13785.

Noudoost, B., & Moore, T. (2011). Control of visual cortical signals by prefrontal dopamine. *Nature, 474*(7351), 372–375.

Price, C. J., & Friston, K. J. (2002). Degeneracy and cognitive anatomy. *Trends in Cognitive Sciences, 6*(10), 416–421.

Rangarajan, V., Hermes, D., Foster, B. L., Weiner, K. S., Jacques, C., Grill-Spector, K., & Parvizi, J. (2014). Electrical stimulation of the left and right fusiform gyrus causes different effects of conscious face perception. *Journal of Neuroscience, 34*(38), 12828–12836.

Rosenke, M., Weiner, K. S., Barnett, M. A., Zilles, K., Amunts, K., Goebel, R., & Grill-Spector, K. (2018). A cross-validated cytoarchitectonic atlas of the human ventral visual stream. *NeuroImage, 170*, 257–270.

Rottschy, C., Eickhoff, S. B., Schleicher, A., Mohlberg, H., Kujovic, M., Zilles, K., & Amunts, K. (2007). Ventral visual cortex in humans: Cytoarchitectonic mapping of two extrastriate areas. *Human Brain Mapping, 28*(10), 1045–1059.

Saalmann, Y. B., Pinsk, M. A., Wang, L., Li, X., & Kastner, S. (2012). The pulvinar regulates information transmission between cortical areas based on attention demands. *Science, 337*(6095), 753–756.

Saygin, Z. M., Osher, D. E., Koldewyn, K., Reynolds, G., Gabrieli, J. D., & Saxe, R. R. (2012). Anatomical connectivity patterns predict face selectivity in the fusiform gyrus. *Nature Neuroscience, 15*(2), 321–327.

Saygin, Z. M., Osher, D. E., Norton, E. S., Youssoufian, D. A., Beach, S. D., Feather, J., … Kanwisher, N. (2016). Connectivity precedes function in the development of the visual word form area. *Nature Neuroscience, 19*(9), 1250–1255.

Schwarzkopf, D. S., Song, C., & Rees, G. (2011). The surface area of human V1 predicts the subjective experience of object size. *Nature Neuroscience, 14*, 28–30.

Song, C., Schwarzkopf, D. S., Kanai, R., & Rees, G. (2015). Neural population tuning links visual cortical anatomy to human visual perception. *Neuron, 85*, 641–656.

Swanson, J. M., Posner, M., Potkin, S., Bonforte, S., Youpa, D., Fiore, C., … Crinella, F. (1991). Activating tasks for the study of visual-spatial attention in ADHD children: A cognitive anatomic approach. *Journal of Child Neurology, 6*, S119–127.

Takemura, H., Rokem, A., Winawer, J., Yeatman, J. D., Wandell, B. A., & Pestilli, F. (2015). A major human white matter pathway between dorsal and ventral visual cortex. *Cerebral Cortex, 26*(5), 2205–2214.

Tallinen, T., Chung, J. Y., Biggins, J. S., & Mahadevan, L. (2014). Gyrification from constrained cortical expansion. *Proceedings of the National Academy of Sciences of the United States of America, 111*(35), 12667–12672.

Van Essen, D. C. (2005). A population-average, landmark- and surface-based (PALS) atlas of human cerebral cortex. *NeuroImage, 28*, 635–662.

Van Essen, D. C., & Dierker, D. (2007). On navigating the human cerebral cortex: Response to "in praise of tedious anatomy." *NeuroImage, 37*(4), 1050–1054; discussion 1066–1058.

van den Hurk, J., Van Baelen, M., & Op de Beeck, H. P. (2017). Development of visual category selectivity in ventral visual cortex does not require visual experience. *Proceedings of the National Academy of Sciences of the United States of America, 114*(22), E4501–E4510.

Wang, L., Mruczek, R. E .B., Arcaro, M. J., & Kastner, S. (2015). Probabilistic maps of visual topography in human cortex. *Cerebral Cortex*, *25*(10), 3911–3931.

Weiner, K. S., Barnett, M. A., Lorenz, S., Caspers, J., Stigliani, A., Amunts, K., … Grill-Spector, K. (2017). The cytoarchitecture of domain-specific regions in human high-level visual cortex. *Cerebral Cortex*, *27*(1), 146–161.

Weiner, K. S., Barnett, M. A., Witthoft, N., Golarai, G., Stigliani, A., Kay, K. N., … Grill-Spector, K. (2018). Defining the most probable location of the parahippocampal place area using cortex-based alignment and cross-validation. *NeuroImage, 170*, 373–384.

Weiner, K. S., Golarai, G., Caspers, J., Chuapoco, M. R., Mohlberg, H., Zilles, K., … Grill-Spector, K. (2014). The mid-fusiform sulcus: A landmark identifying both cytoarchitectonic and functional divisions of human ventral temporal cortex. *NeuroImage, 84*, 453–465.

Weiner, K. S., & Grill-Spector, K. (2010). Sparsely-distributed organization of face and limb activations in human ventral temporal cortex. *Neuroimage, 52*(4), 1559–1573.

Weiner, K. S., Yeatman, J. D., & Wandell, B. A. (2017). The posterior arcuate fasciculus and the vertical occipital fasciculus. *Cortex, 97*, 274–276.

Weiner, K. S., & Zilles, K. (2016). The anatomical and functional specialization of the fusiform gyrus. *Neuropsychologia, 83*, 48–62.

Witelson, S. F. (1992). Cognitive neuroanatomy: A new era. *Neurology, 42*(4), 709–713.

Witthoft, N., Nguyen, M. L., Golarai, G., LaRocque, K. F., Liberman, A., Smith, M. E., & Grill-Spector, K. (2014). Where is human V4? Predicting the location of hV4 and VO1 from cortical folding. *Cerebral Cortex, 24*(9), 2401–2408.

Yeatman, J. D., Rauschecker, A. M., & Wandell, B. A. (2013). Anatomy of the visual word form area: Adjacent cortical circuits and long-range white matter connections. *Brain and Language, 125*(2), 146–155.

Yeatman, J. D., Weiner, K. S., Pestilli, F., Rokem, A., Mezer, A., & Wandell, B. A. (2014). The vertical occipital fasciculus: A century of controversy resolved by in vivo measurements. *Proceedings of the National Academy of Sciences of the United States of America, 111*(48), E5214–23.

Zilles, K., Schleicher, A., Langemann, C., Amunts, K., & Morosan, P. (1997). Quantitative analysis of sulci in the human cerebral cortex: Development, regional heterogeneity, gender difference, asymmetry, intersubject variability and cortical architecture. *Human Brain Mapping, 5*, 218–221.