

Cortical Gradients and Their Role in Cognition

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Glossary

Connectivity space A coordinate space that represents the variation in connectivity patterns along its dimensions.

Connectotopies The consistent topographic organization of connectivity across distinct regions.

Intrinsic cortical geometry Spatial relationships within the cortex based solely on the properties of the surface itself.

Functional connectivity Temporal correlation of spontaneous brain activity (often measured using fMRI).

Gradients Gradual changes in features that are continuous in space.

Topographic connectome The spatial arrangement of connections in the brain.

Introduction

Toward the end of the 19th century, several fields of research converged on similar problems without recognizing how related their respective questions actually were. Geologists were perplexed by observations of similar granite formations and glacier deposits in both Africa and South American, while paleontologists had no explanation for the fossils from matching Triassic species found across several continents. It took an independent researcher, Alfred Wegener, to recognize that the spatial dynamics of the earth's surface could provide a common answer across these disparate disciplines. By proposing the theory of continental drift (Wegener, 1912), Wegener offered a model that not only accounted for each of these phenomena, but crucially managed to link these fields through a common underlying model of tectonic spatial dynamics.

In the field of human brain mapping, we have unprecedented ability to map numerous features of the cerebral cortex — maps of function, connectivity, cortical microstructure, gene expression, and others. And we now have the capabilities and data to track brain growth longitudinally, compare populations, and conduct heritability studies. Striking to anyone familiar with the spatial patterns arising from these fields is the frequent convergence across different imaging modalities, clinical populations, and functional states. Although the explosion of novel techniques and methodologies across the expanse of human brain mapping has pushed the field toward ever increasing specialization, just as in the prior historical example, ample convergence can be found in pursuing the question of how the human brain arrived at its spatial form.

Over half a century ago, Friedrich Sanides, who was trained in traditional techniques of cortical histology by Cecile and Oscar Vogt, possessed substantial knowledge regarding the locations of various cortical areas based on both cyto- and myeloarchitectonic mapping techniques. By mid-century, faced with numerous maps of the cerebral cortex from a diverse set of mammalian species, he posed a simple question that would guide the rest of his research career: Why do cortical areas arrive at their specific locations?

Sanides thus embarked on several decades of comparative studies of cortical phylogeny, describing a stepwise progression in the laminar differentiation of the cerebral cortex, which he termed the “dual origin theory of the cerebral cortex” (Sanides, 1962; Pandya et al., 2015). Through his observations of how the cortical layer structure increased in complexity during mammalian cortical evolution, and by rooting those observations in the spatial arrangement of cortical areas, Sanides developed a map — or more accurately, a series of maps throughout his career — that proposed the spatial trajectories of how cortical areas emerged during

the evolution of the mammalian cerebral cortex. Much like Wegener, Sanides argued that an understanding of the human brain requires a phylogenetic model that builds from the history of its spatial dynamics. And much like Wegener, Sanides' theories were not all confirmed. Nevertheless, his basic question provides a fertile point of departure for the present moment in human brain mapping, when the convergence across disparate imaging fields calls for unifying models that reduce the brain's complexity to principles of organization.

Is there a spatial principle governing the arrangement of connectivity and functions throughout the cerebral cortex? This chapter summarizes a recent line of research aimed at characterizing such spatial gradients in cortical organization. We begin with observations regarding the distribution of connectivity distances, which correspond to a region's distance from primary sensory/motor areas (Oligschlager et al., 2017). To map the spatial distribution of connectivity patterns in a data-driven manner, we next describe a methodology for decomposing a connectivity matrix into a set of spatial gradients that capture connectivity patterns. We then proceed to focus on the first dimension of this decomposition, which we term the "principal gradient" (Margulies et al., 2016), that describes an axis spanning from unimodal sensory/motor cortex to transmodal regions. The following section delves further into the implications of this organization for models of cognition. We discuss mechanisms that may underlie the relationship of local processing to large-scale cortical structure. Building on this perspective, we propose these geometric relationships may constitute the building blocks of a cortical coordinate system (Huntenburg et al., 2018) as a basis for characterizing the functional consequences of macroscale cortical anatomy.

In the final section we consider the broader implications of these large-scale organizing principles for cognitive neuroscience as well as current and future applications of these schemas to developmental and clinical disorders. By mapping the distributed patterns of functional specialization and outlining potential neurobiological mechanisms from which they emerge, this line of research contributes to the agenda established by Sanides and others toward uncovering the blueprints underlying cortical organization, and eventually toward a deeper understanding of how brain structure both enables and constrains our cognitive repertoire.

Spatial Trends in Cortical Organization

Delineating boundaries within the cerebral cortex has been one of the central research endeavors within human neuroscience since the inception of the field over a century ago. While establishing the criteria for what constitutes a cortical area continues to be debated (Eickhoff et al., 2018; Van Essen and Glasser, 2018), there is general consensus regarding the features that can be used to differentiate one area from the next (Van Essen and Glasser, 2018). However, taking a global perspective on the cortical mosaic allows us to ask the broader question of why are areas and networks are spatially distributed as they are. If there is indeed an overarching arrangement of cortical features on a global-level, the complexity of spatial layout could be captured by a more parsimonious set of spatial patterns.

Connectivity Distance From Primary Unimodal Areas

In an effort to account for the dramatic expansion of association cortex in the human brain, Buckner and Krienen introduced the 'tethering hypothesis' (Buckner and Krienen, 2013), which proposes that association cortex emerges by virtue of its distance from the molecular gradients that determine the specialization of primary areas during cortical ontogeny. Left unspecialized early in cortical development, the feature that eventually establishes the role of association cortex is its long-distance connections. Given the spatial basis of this hypothesis, one implication would be a precise relationship between how far an area is located from primary cortex and the distance of its connections. In other words, the further a region is untethered, the longer its connections to regions that are equally distant.

By calculating the distance between connected points along the human cortical surface, we found a continuous increase in connectivity distance from primary areas toward a set of regions within association cortex referred to as the default-mode network (Gusnard et al., 2001; Shulman et al., 1997; Buckner et al., 2008; Greicius et al., 2003), where connectivity distance was furthest (Oligschlager et al., 2017). As this result confirms prior work regarding the distribution of connectivity distance (Sepulcre et al., 2010), we then further investigated whether the spatial location with respect to primary areas could account for these observations.

Noteably, in all but rostral prefrontal cortex, we found there to be a significant spatial correlation between distance-from-primary and connectivity distance. Given the limited explanatory power of the distance-from-primary-areas to account for prefrontal spatial arrangement, in the following section we describe a line of work in which we reverse the hypothesis: Rather than the layout of association cortex resulting from its distance from primary areas, we hypothesize that the anchor lies rather within association cortex, with distance from regions of the default-mode network providing the dominant organizing principle.

Mapping Gradients in Cortical Organization

When the gradual change in a feature — such as altitude along a terrain — is continuous in space, we can describe it as a gradient. In the context of brain organization, this mapping of the continuous changes between a feature space and anatomical space is the aim

of characterizing gradients. Classical examples from neuroanatomy are found in the sensory/motor topographies within primary cortex. For example, the visual field is mapped continuously, preserving spatial structure in its cortical representation (Wandell et al., 2007). Likewise, primary somatosensory cortex preserves continuity of body representation (Penfield and Boldrey, 1937), and primary auditory cortex is structured along the frequency spectrum (Striem-Amit et al., 2011). Extending this framework to connectivity enables the mapping of where the progression along the cortical surface follows corresponding changes in connectivity patterns.

The term *topographic connectome* was introduced in 2013 by Jbabdi and colleagues to describe the organized spatial transformations between connections of different brain regions (Jbabdi et al., 2013). More recently, Haak and colleagues introduced the term *connectopies* to refer to shared spatial variation in functional connectivity (Haak et al., 2018), and Mars and colleagues introduced *connectivity space* to describe the representation of connectivity patterns in a low-dimensional embedding (Mars et al., 2018). However, even before these terms were introduced, several studies demonstrated continuous spectra of connectivity within cortical structures such as the insula (Cerliani et al., 2012) and temporal lobe (Bajada et al., 2017; Qin et al., 2016). At the network-level, an ordered and repeating stepwise pattern across the distributed perisylvian language networks has been demonstrated (Xiang et al., 2010; Margulies and Petrides, 2013), and association networks have also been noted to lay in repeated spatial orderings (Power et al., 2011; Blumenfeld et al., 2013). While the current chapter focuses predominantly on connectivity between neocortical areas, extensive connectivity topographies have also been observed within the hippocampus (Strange et al., 2014; Vos de Wael et al., 2018), entorhinal cortex (Navarro Schroder et al., 2015), thalamus (Lambert et al., 2017; Yang et al., 2020), cerebellum (Guell et al., 2018), and between the striatum and cerebral cortex (Haber, 2003; Marquand et al., 2017). In the few years since the concept was formalized for the human neuroimaging literature (Jbabdi et al., 2013; Haak et al., 2018), a rapid output of research is providing a more thorough portrait of how connectivity patterns are interrelated across regions.

The complexity of brain connectivity can be reduced analytically using a small set of dimensions that capture the most prevalent patterns of variation. To achieve this low-dimensional representation of the connectivity matrix, nonlinear dimensionality reduction approaches, such as Laplacian eigenmaps (Cerliani et al., 2012; Haak et al., 2018) and diffusion map embedding (Nenning et al., 2017; Langs et al., 2015) have been the widely used. However, it should be noted that recent work demonstrates similar results can be derived using linear approaches such as principal component analysis (Hong et al., 2020; Vos de Wael et al., 2020).

The first two connectivity gradients replicate a theory of global cortical organization in which regions of the human cerebral cortex are hypothesized to be organized along two core dimensions: segregation of unimodal sensory and motor systems and hierarchical integration toward transmodal regions (Mesulam, 1998a, 2008) (Fig. 1A). The results of a data-driven approach converge on similar observation (Fig. 1B). While the second component differentiates somatosensory/motor from visual systems, the first component of the connectivity space — accounting for the maximum variance, and which we refer to as the *principal gradient* — reveals a spectrum of organization from primary visual and somatosensory/motor areas to transmodal association cortex (Fig. 1C). These latter regions correspond to regions known in the human brain as the default-mode network (Gusnard et al., 2001; Shulman et al., 1997; Buckner et al., 2008; Greicius et al., 2003).

Resting-state networks describe functional systems (Smith et al., 2009), and the broad acceptance of a set of canonical networks has infused cognitive neuroscience with a new common vocabulary for parsing brain function (Yeo et al., 2011; Power et al., 2011). Nevertheless, establishing the appropriate number of networks for accurately describing subdivisions of the cerebral cortex remains a methodological challenge. In part, this may be due to smooth transitions between networks, which complicate the goal of delineating sharp and consistent parcellations. Projecting the seven canonical networks (Yeo et al., 2011) onto the principal gradient reveals an arrangement into categories of unimodal (visual, somatosensory), cognitive/attention (dorsal attention, salience), followed by the frontoparietal control network, and finally the default-mode network. Recent findings in high-resolution individual-level network mapping have also confirmed this network ordering along the cortical surface (Braga and Buckner, 2017).

To investigate the question posed earlier of whether distance from default-mode network accounts for the spatial distribution of connectivity patterns, we mapped the distance along the cortical surface from the transmodal apex regions. The results reveal a spatial pattern that is highly consistent with principal gradient itself, where the equidistant meeting point between the transmodal regions precisely align with the morphological landmarks of primary sensory areas (Fig. 1D).

This spatial arrangement informs our understanding of why networks are spatially distributed as they are, and it provides a foundation for considering their functional roles along a continuum. This is germane to understanding the default-mode network, as since its discovery, the field has struggled to reconcile its role in cortical processing with its rogue response profile — namely, that it decreases in activity during a wide-range of externally-oriented task demands (Gusnard et al., 2001; Shulman et al., 1997; Buckner et al., 2008; Fox et al., 2005). By situating the default-mode network at the apex of a unimodal–transmodal spectrum, rather than interpreting its role in opposition to cognitive task performance, we can begin to consider its function along a global cortical hierarchy.

Functional Implications of Gradient Organization

The shift from a network-based framework to describing connectivity within a continuous space opens up new challenges for integrating such perspectives into the language of cognitive neuroscience. It is noteworthy that at opposite ends of the functional spectrum are areas involved in perception of environmental input and regions involved in higher-order memory functions, which

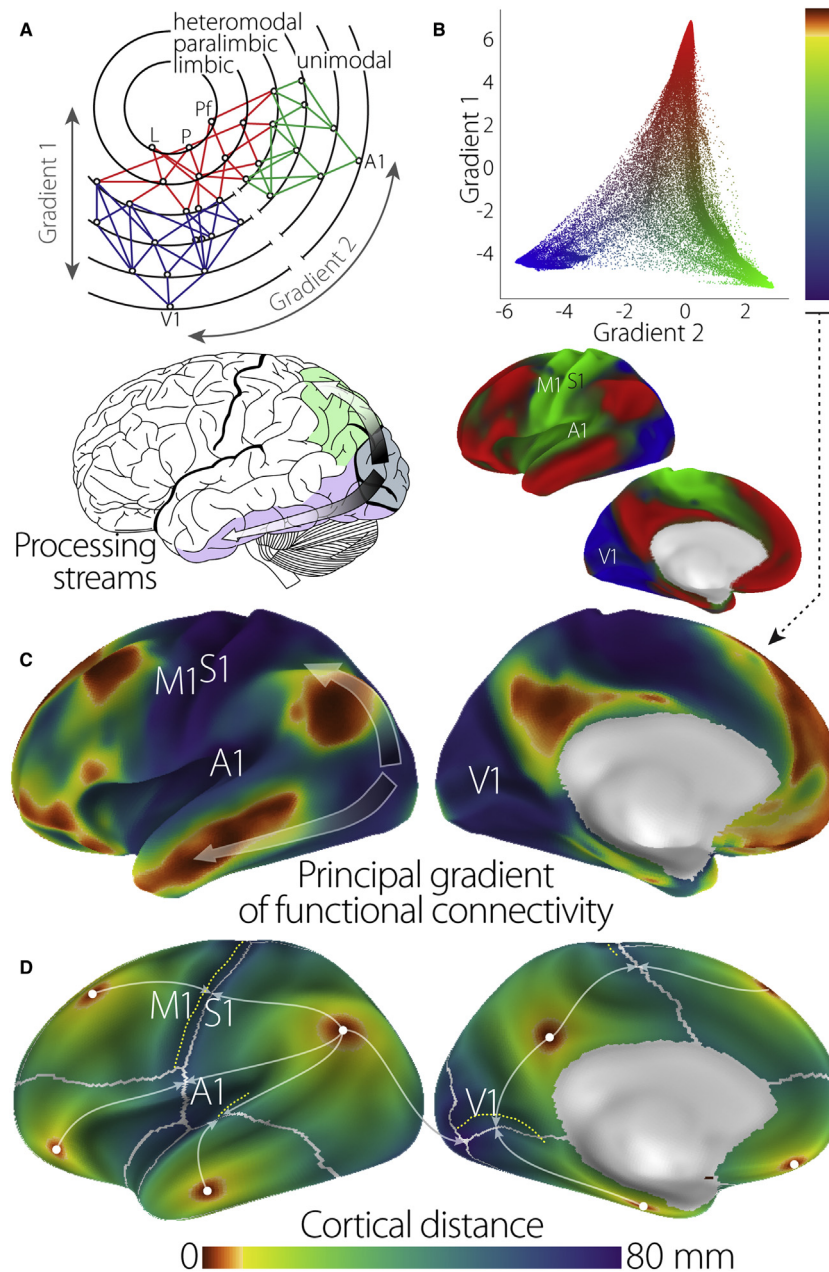


Figure 1 The global hierarchy model (A) proposed by Mesulam (1998a) is captured by first two functional connectivity gradients (B). The first dimension, termed the principal gradient (C), describes an axis from primary areas (blue) to transmodal regions (red), which converges with spatial distance along the cortical surface from transmodal regions (D). Figures modified from Margulies et al. (2016), and Selket (https://commons.wikimedia.org/wiki/File:Ventral-dorsal_streams.svg), "Ventral-dorsal streams", <https://creativecommons.org/licenses/by-sa/3.0/legalcode>.

aligns with the dual-origin theory division of sensory- and memory-related areas (of piriform (olfactory) and hippocampal cortex) described by Sanides and others (Sanides, 1962, 1964; Abbie, 1940; Dart, 1934; Pandya et al., 2015). Taken together, we could interpret the principal gradient as capturing an axis of phylogenetic expansion that is conserved from this early mammalian blueprint. In addition, recent work has suggested that the global cortical hierarchy proposed by Mesulam (1998b) may represent the foundation of a predictive coding hierarchy (Chanes and Barrett, 2016; Barrett and Simmons, 2015), where, reformulated in the context of the principal gradient, predictions regarding the environmental stimuli are sent down along the gradient, and incoming information is sent up in the form of prediction error.

The principal gradient may describe a global hierarchy — not the only hierarchy present in the cerebral cortex (Felleman and Van Essen, 1991; Buckner and Krienen, 2013; Hilgetag and Goulas, 2020), but a prominent stream that establishes the hierarchical relationship integrating perceptual experience into the higher-order concepts, memories, categories, and abstractions that in turn sculpt those incoming perceptual experiences. Results of a meta-analysis of functions along the principal gradient demonstrates

increasingly abstract and memory-related functions toward the transmodal-end of the gradient, setting these in opposition to the unimodal functions of sensory/motor cortex. This observation is in line with the perceptual decoupling hypothesis, which proposes that memory retrieval requires a process of decoupling from sensorimotor systems to enable cognition to generate content that is independent of our surrounding environment (Smallwood, 2013). This finding has also been confirmed by a series of studies probing the functional processes mediated by the opposing extremes of the principal gradient spectrum (Murphy et al., 2017, 2018).

Relevance of Local Cortical Geometry for Global Function

At the heart of this research question is the aim of discerning principles to account for the distribution of functional specialization across the cerebral cortex. But what does an understanding of this spatial arrangement offer to our understanding of function? When mapping the cerebral cortex as a modular system, each cortical area can be considered as an independent unit with specific computational characteristics and interareal connections that define its location in the broader processing hierarchy. And were cortical areas unconstrained by the biological contingencies of development and evolution, one could imagine the areas of the cortex as tiles arranged in the interest of optimizing function. Each area, independent from others, could be positioned to minimize wiring cost (Chen et al., 2013; Raj and Chen, 2011; Cherniak et al., 2004), and therefore transmission speed. Or areas could be arranged to ensure local redundancy, such that any location on the cortex contained all the necessary components to ensure the preservation of functions in the event of damage. Numerous other heuristics could be used to optimize cortical layout, but they depend on treating cortical areas as modular and separable as mosaic tiles.

The ontogeny of the cerebral cortex provides a critical constraint on its spatial layout. Whether through gradients in gene expression and morphogens (Tiberi et al., 2012; Borello and Pierani, 2010; Sansom and Livesey, 2009), biophysical mechanical constraints (Toro and Burnod, 2005), or temporal dynamics of development (Kaiser, 2017), numerous evolutionary and developmental factors result in the spatial distribution of cortical features of a given species. Given the consistent blueprint of the nervous system across vertebrates (Nieuwenhuys, 2017; Nieuwenhuys and Puelles, 2016), and the generally consistent layout of the cerebral cortex across mammalian species (Krubitzer, 2007, 2009), it is possible to track the spatial emergence of new features as the cortex expands from one species to another — and these constraints ensure that the embedding of the brain in physical space plays a critical role in its function.

One general principle that converges with our findings is the anatomical proximity of similar functions. Elkhonon Goldberg previously described this as a ‘spatial-functional isomorphism’ (Goldberg, 1989). In his gradient model of neocortical organization, Goldberg theorizes the layout of higher-order functions is intertwined with the relative locations of primary cortical areas. While he predicted observations regarding the intrinsic geometry of the cortex, further aspects of local communication would be necessary for cortical topology to be a viable substrate for establishing the predictive functional features of the cortex.

Long-distance connections receive disproportionate research attention considering their relative sparsity in the cerebral cortex (van den Heuvel and Sporns, 2011). The vast majority of axons connect local areas, with connectivity density following an exponential decay with distance (Ercsey-Ravasz et al., 2013). Nevertheless, as long-distance connections come with high wiring-cost and their presence is critical to healthy brain function (Goulas et al., 2015; Hilgetag and Goulas, 2016), the majority of research into connectivity organization with the cerebral cortex is dedicated to this set of connections. However, given that the majority of connections rather represent local interactions, thereby following the local intrinsic geometry of the cortex, it is plausible that cortical layout plays a critical role in determining function at a global scale. In other words, how might cortical geometry provide a foundation for large-scale organization?

The relationship between large-scale systems and local cortical layout offers an entry point for mapping between the mesoscopic and macroscopic scales of cortical function (Mitra, 2014). As we have previously described the observation that cortical specialization is related to the intrinsic geometry of the cortical surface, how might this spatial relationship contribute to the mechanics of cortical processing? Prior work has interpreted intrinsic geometry as reflecting local processing (Ecker et al., 2013; Paquola et al., 2020), and the terrain for local spreading dynamics (Misic et al., 2015). Horizontal non-myelinated fibers can extend several millimeters within supragranular cortical layers, and have been observed in primary areas (Angelucci et al., 2002) as well as prefrontal (Lewis et al., 2002; Melchitzky et al., 2001). This microstructural property has the capacity to provide the substrate for information propagation in the form of traveling waves (Muller et al., 2018). Waves in the alpha and theta range propagate at 0.25–0.75 m/s (Zhang et al., 2018), and may organize neural processing within continuous portions of the cortex. At the lower frequencies captured by functional MRI, the propagation of activity in the form of traveling waves has been observed in several recent studies in both humans and animal models (Mitra et al., 2014, 2015a,b, 2017, 2018; Mitra and Raichle, 2016, 2018; Majeed et al., 2009, 2011; Roberts et al., 2018). Were this spatial propagation to play a significant role in coordinating cortical function, the precision we observe in the relative spatial positions of interconnected regions could certainly be one of its key developmental consequences.

Basis of an Intrinsic Coordinate Space

A common language for referencing positions on the cortical surface enables standardization across datasets and studies. Standardizing space nevertheless remains a challenge, as the widely used templates of the cerebral cortex, such as the MNI152 stereotaxic

space and the fsaverage cortical surface space, remain based in coordinate systems that are entirely dependent on the geometry of the brain. While these coordinate systems offer a valuable service to the field, they remain limited by only describing spatial positions. Several coordinate systems for the cerebral cortex based on intrinsic geometry and morphological features have also been developed (Toro and Burnod, 2003; Lefevre et al., 2018; Van Rooij et al., 2018; Le Guen et al., 2018; Auzias et al., 2016). These examples establish two-dimensional projections, and while they constitute a major advance for providing a meaningful set of coordinates that represent consistent morphological features across individuals, the coordinates themselves, being entirely derived from morphology, are limited to describing functional trends that follow topography of the cortical surface. A contrasting example, albeit for deep brain structures, is the natural coordinate system (Nieuwenhuys and Puelles, 2016), in which the coordinates are derived from spatial dimensions that capture the evolutionary history of the nervous system. Thus, position in the natural coordinate system is informative regarding the phylogeny of the structure as well as functional roles.

The advantage of a coordinate system based on multimodal features that are relevant to function is that the space that is meaningful for cortical processing may not be the physical space in which it is embedded (Mars et al., 2018). For example, a connectivity-defined space can offer a parsimonious differentiation of functional states (Karapanagiotidis et al., 2020). We recently proposed that the intrinsic geometry of the cortex along the unimodal–transmodal gradient provides a meaningful contribution to a cortical coordinate system (Huntenburg et al., 2018). Based on the two-dimensional representation of global processing hierarchies (Mesulam, 1998a, 2008), we can extend this theory by incorporating the convergence with intrinsic cortical geometry to construct a coordinate space. One limitation of this approach is that coordinates are not all unique, as the two dimensions are only orthogonal in the connectivity space. However, the advance proposed here is a system that incorporates distinct features such as connectivity, function, and microstructure.

Applications to Clinical Disorders

Topographic gradients, which are central to the organization of sensory/motor areas, reorganize following damage to their respective systems (Pons et al., 1991). For example, in the somatosensory domain, expansion of adjacent body parts' representations is evident after spinal cord injuries and amputations (Flor et al., 1995; Florence and Kaas, 1995), and impairment can be manifest as discontinuity of local gradients within somatosensory cortex (Saadon-Grosman et al., 2015). It is plausible that reorganization across association cortex may also be reflected in alterations of the connectivity space.

As the brain is not composed of isolated, discrete units, neuropathologies rarely impact one region or network in isolation. By gaining a deeper understanding of patterns of disease propagation (Zheng et al., 2019), the approaches described here have the potential to better mitigate the existing gaps between symptomatology and brain function. Gradients based on connectivity and cortical microstructure may compactly represent neurodevelopmental processes (Paquola et al., 2019; Ball et al., 2020) and brain changes during aging (Lowe et al., 2019; Bethlehem et al., 2020). In the study of clinical indications related to both atypical neurodevelopment (Hong et al., 2019; Lariviere et al., 2020; Dong et al., 2020a; Park et al., 2020) or localized lesions (Bayrak et al., 2019), these approaches may furthermore increase our understanding of perturbations to the system as a whole. For example, these approaches have provided a basis for the discovery of a perturbation of the principal gradient in individuals with autism spectrum disorder, which we interpret as a dysfunction of the cortical hierarchy (Hong et al., 2019). Other directions which may prove fruitful include investigating the connectivity gradients in attention-deficit/hyperactivity disorder, which has already been characterized by alterations in sensory processing streams (Carmona et al., 2015; Pretus et al., 2019), and schizophrenia (Tian and Zalesky, 2018), which has been characterized by disruption of the hierarchy between sensory perception and top-down priors (Fletcher and Frith, 2009; Dong et al., 2020b).

Future Considerations

While connectivity gradients inherently represent continuous variance across the cerebral cortex, the question persists of whether the building blocks of the cerebral cortex, especially within higher-order association regions, are discretely divided or continuous in nature. The traditional macroscale units of cortical processing are considered to be cortical areas, which can be defined as performing similar operations on incoming signal. However, recent evidence from studies of face processing in the temporal lobe has demonstrated a topographic organization of feature mapping (Chang and Tsao, 2017), lending support to the notion that, rather than discrete areas, local gradients may also constitute units of cortical processing. We have thus far aimed to focus our attention on the large-scale trends and spatial patterns across the cortex, maintaining an agnostic position regarding the nature of local transitions between distinct areas. Our decision to side-step this important research question was based in it remaining a long-standing and highly controversial research question (Bailey and Bonin, 1951), and one which may not be adequately addressed using the relatively low-resolution of MRI data — even though methods capable of capturing gradual transitions are in development (Huth et al., 2015, 2016; Tian and Zalesky, 2018). Nevertheless, the question of continuous versus discrete boundaries along gradients remains a research topic with the future potential to dramatically impact our understanding of cortical processing and cognitive function.

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