



Editorial

Gradients in brain organization

1. Introduction

Complementary to the progress that has been made in the identification and mapping of discrete brain areas (Amunts et al., 2020; Genon et al., 2021) and macroscopic functional communities (Eickhoff et al., 2018b; Schaefer et al., 2018; Yeo et al., 2011), recent years have seen a rise of new methods and applications to study spatial transitions — or *gradients* — of brain organization (Haak and Beckmann, 2020; Haak et al., 2018; Huntenburg et al., 2018; Margulies et al., 2016; Vos de Wael et al., 2020). Already emphasized by early analyses of *post mortem* cytoarchitecture in humans and non-human primates (Bailey and Bonin, 1951; Sanides, 1962; Von Bonin and Bailey, 1947), recent neuroimaging and network neuroscience studies have made significant progress in the mapping of spatial gradients in the human and non-human brain.

Such gradients have been described across multiple aspects of brain organization, including MRI-based measures of cortical morphology and microstructure (Demirtas et al., 2019; Huntenburg et al., 2017; Paquola et al., 2019b; Wagstyl et al., 2015), indices of functional and structural connectivity (Margulies et al., 2016; Oligschläger et al., 2017; Vos de Wael et al., 2021), as well as task-based activation and deactivation patterns (Caciagli et al., 2021). Overall, these studies suggest confluent spatial trends of neural organization in which structure-function relationships can be investigated. For example, one key study in humans and non-human primates based on resting-state fMRI analysis demonstrated a principal axis of functional differentiation between sensory and heteromodal systems (Margulies et al., 2016), which closely corresponded to models of the primate cortical hierarchy (Mesulam, 1998) and furthermore showed that heteromodal networks such as the default mode network are maximally spatially distant from sensory systems. In parallel, a mounting literature has shown evidence for similar gradients at the level of gene expression patterns (Burt et al., 2018; Goulas et al., 2019c; Seidlitz et al., 2019; Vogel et al., 2020) as well as receptor architecture (Hansen et al., 2021), suggesting that gradients may offer a framework to interrogate the interplay between brain structure, metabolism, and function. Studying microstructural and functional gradients in developmental and aging cohorts has furthermore provided insights into lifespan changes in the spatial layout of brain organization (Baum et al., 2020; Bethlehem et al., 2020; Paquola et al., 2019a; Park et al., 2021a; Sydnor et al., 2021). Such approaches may ultimately lead to better understanding of brain changes seen in prevalent neurological and neuropsychiatric conditions (Benkarim et al., 2021; Fadaie et al., 2021; Li et al., 2021; Park et al., 2021b, 2021d; Tian et al., 2019; Dong et al., 2020). Finally, by providing a continuous coordinate system to characterize topographic organization and structure-

function relationships in humans and non-human animals (Buckner and Krienen, 2013; Fulcher et al., 2019; Huntenburg et al., 2018), the identification and analysis of brain gradients promises to advance theories and knowledge of brain evolution.

This Special Issue aims to reflect the rapidly expanding literature on brain gradients and to gather the growing community working on this topic. A total of 36 articles (Fig. 1) cover (i) novel methods to study brain gradients and to evaluate their ability to capture inter-individual differences in brain organization, (ii) the ability of gradients to inform multiscale and multimodal anatomical investigations, also contextualizing gradient mapping with more established approaches to understand cortical arealization, (iii) the role of gradients in brain dynamics and cognition, and finally (iv) the utility of gradients as a framework to analyze and conceptualize brain evolution and development. In what follows, we highlight the articles of this Special Issue within these broad themes.

2. Methodological advances in gradient mapping

The remarkable growth in our capacity to map local and whole-brain cortical gradients as novel ways to study both subregional as well as macroscale brain organization has been tied to the introduction of new analytic techniques. These include methods to derive gradients (Guell et al., 2018; Haak et al., 2018; Margulies et al., 2016; Vos de Wael et al., 2020), to align them to one another (Benkarim et al., 2021; Nenning et al., 2015, 2020; Vos de Wael et al., 2020; Xu et al., 2020), to analyze gradient-derived features (Haak et al., 2018; Langs et al., 2015; Tian et al., 2020), and to assess their associations to neural as well as non-neuronal spatial maps (Alexander-Bloch et al., 2018). A series of papers in this special issue provide useful additions to the growing arsenal of gradient analysis.

Describing gradients requires a class of techniques that can characterize gradual changes in features. Bajada et al. (2020) introduce the Vogt-Bailey (VB) index, which quantifies across the cortical mantle on how sharply inter-areal boundaries are defined and released open tools for VB index calculation and gradient mapping (<https://github.com/VBIndex/>). Arguing for potential benefits of a gradient perspective for functional cartography, Haak and Beckmann (2020) outline that gradient models may capture both functional heterogeneity as well as functional multiplicity across the cortical mantle, and thus complement arealization approaches that posit discrete boundaries and assume functional uniformity within regions. In Glomb et al. (2020), the authors present a graph signal processing framework that, applied to EEG data, identifies harmonic basis functions to compactly describe neurophysiological brain activity. These harmonics are or-

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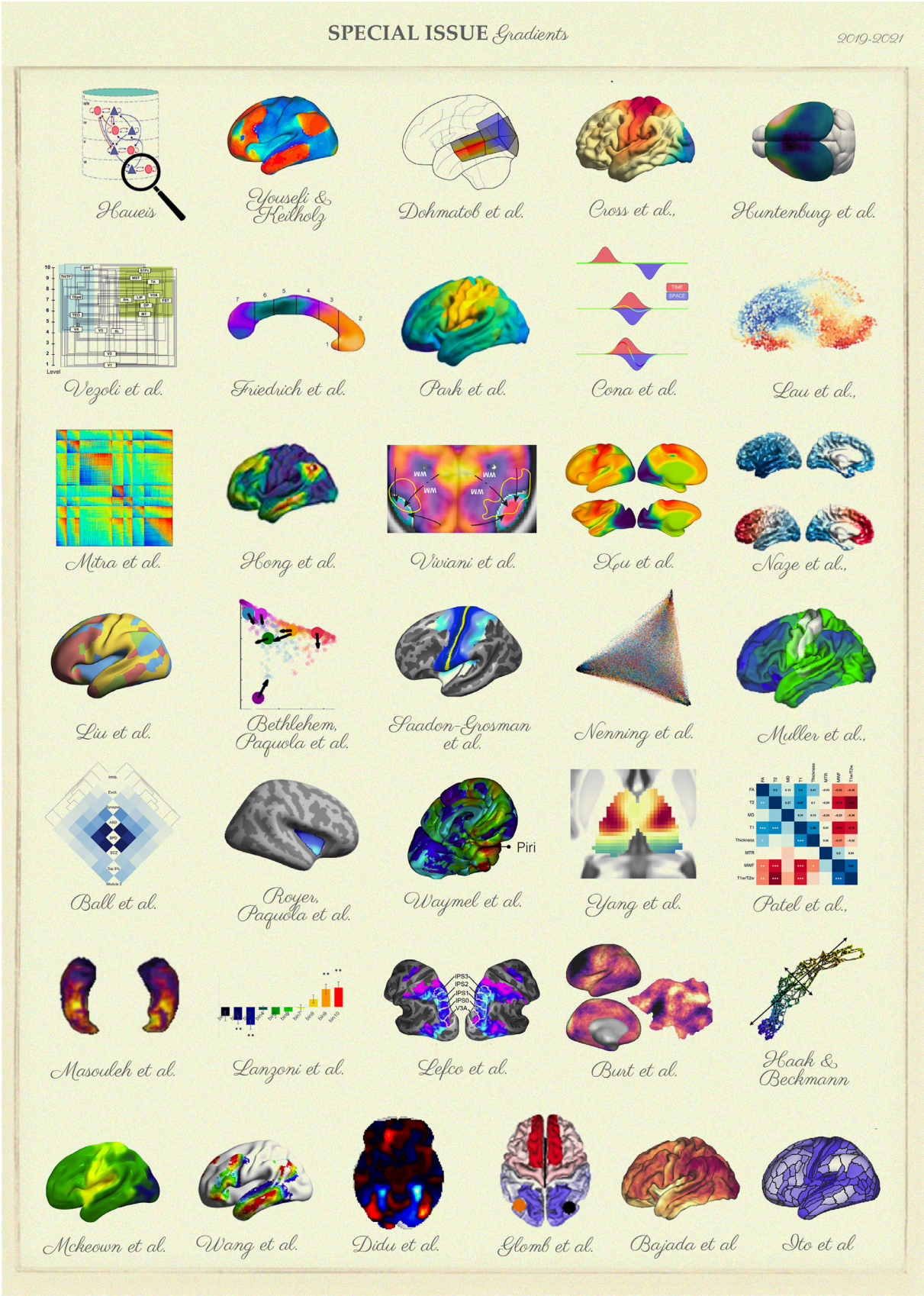


Fig. 1. The 36 articles covered in the special issue.

dered by the degree of smoothness/variation along the cortex, leading to a multi-scale representation of brain connectivity. They demonstrate that the sparse harmonics representation with only a few components can track large-scale cortical activity during a face detection task. [Dohmatob et al. \(2021\)](#) study the predictability of task fMRI contrast data from resting fMRI. They demonstrate that the combination of data from multiple parcellations is the best representation of local functional gradients, offering highest performance in rest-to-task mapping. Using a sparse matrix factorization algorithm trained on multiple, diverse fMRI datasets [Dadi et al. \(2020\)](#), Dadi and colleagues identify a novel dictionary of fine-grained high-dimensional functional modes for fMRI representation.

Building on the description of fundamental patterns, a major challenge is to characterize meaningful population variance. To advance the analysis of data across multiple individuals, [Nenning et al. \(2020\)](#) propose a joint embedding procedure. Comparing a joint embedding approach applied to resting-state fMRI data to conventional orthonormal/Procrustes alignment, they demonstrate higher discriminability of individual subjects, higher overlap between resting-state fMRI derived topographies and task-fMRI activations, as well as an enhanced prediction of age. Overall, these findings suggest that joint embedding may enhance the study of inter-individual differences in a gradient setting, and thus potentially enhance its ability to serve as biomarkers. In a similar vein, [Hong et al. \(2020\)](#) evaluate strategies to improve the reproducibility, reliability and predictive validity of resting-state fMRI gradients. Their study provides several recommendations to enhance reproducibility and reliability, and they demonstrate that the low-dimensional connectivity gradient approaches can outperform conventional edge-based analyses in terms of predicting phenotypic scores based on the human connectome dataset.

In addition to deriving lower dimensional representations of functional or structural data, the field is increasingly exploring new formal ways to contextualize MRI-derived measures with other markers of neural architecture. [Patel et al. \(2020\)](#) present a virtual histology approach, relating different MRI measures with *post mortem* gene expression data. They report that many MRI measures, including T1 and T2 relaxation times, T1w/T2w ratio, MWF, MTR, FA and cortical thickness reflect expression profiles of genes specific to CA1 pyramidal cells; genes enriched in processes related to dendritic arborization. In [Burt et al. \(2020\)](#), the authors present an autocorrelation preserving null model and corresponding open access software (<https://github.com/murraylab/brainsmash>), which can help to statistically evaluate the correspondence between gradients and other aspects of brain organization while controlling for autocorrelation. Expanding even further upon the search for correspondence of different imaging features, [Haukeis \(2021\)](#) advocates for the use of formal multi-scale models, which could provide a mechanistic link between microcircuit organization and macrolevel brain function.

2.1. Advancing multiscale neuroanatomy and structure-function exploration

By offering a continuous perspective to assess subregional heterogeneity, to arrange cortical areas along axes of whole-brain organization, and to interrogate structure-function relationships, gradient mapping may advance cortical cartography, and thus inform and complement established perspectives on cortical arealization ([Genon et al., 2021](#); [Eickhoff et al., 2018a](#)). The Special Issue includes several papers that provide important proof of principle for the utility of continuous representations in characterizing cortical areas and networks.

On a whole-brain scale, gradients appear to map the global relationships between distributed functional systems as well as how spatial features of specific systems map are situated within broader patterns of organization. And while sensory systems, such as the visual and auditory domains, have long been the focus of research into domain-specific hierarchies — often described as stepwise processing streams

— the methodologies and frameworks afforded by a gradient-based perspective enable insight into other domains. For example, the somatosensory system demonstrates three processing hierarchies extending away from the central sulcus ([Saadon Grosman et al., 2020](#)). The authors combine tactile body stimulation and fMRI measurements to identify functional gradients in somatosensory areas. By stratifying response patterns with respect to laterality and selectivity, they furthermore show correspondence between gradients and a functional hierarchy of somatosensory representations. [Lefco et al. \(2020\)](#) examine gradients of frontoparietal network organization, combining analysis of visual attention and visual short-term memory fMRI tasks with resting-state fMRI connectomics. Their findings reveal fine-scale gradients in functional connectivity within the frontoparietal visual network.

Focussing on the insula, a paralimbic cortical region, [Royer et al. \(2020\)](#) study microstructural gradients based on myelin-sensitive MRI analysis. They report dominant axes of subregional microstructural organization, one running in anterior-posterior direction and one differentiating the dorsal anterior subdivision from the remaining insular cortex. In addition, they show associations to underlying histological characteristics and large-scale functional network connectivity, suggesting that microstructural variations can help to understand functional diversity in integrative hub regions such as the insula. Assessing another nexus in the human limbic system, [Kharabian Masouleh et al. \(2020\)](#) study gradients of structural covariance in the hippocampus, a structure in the mesiotemporal lobe. They demonstrate a principal gradient running along the hippocampal long axis that closely follows its main axis of functional differentiation, and a second gradient that runs along dorsal ventral axes that reflects hippocampal microstructural differentiation. Also investigating the architecture of paralimbic areas, [Waymel et al. \(2020\)](#) associate different functional gradients with meta-analytical activations from episodic memory and olfactory tasks, and show that the first, sensory-transmodal functional gradient relates most strongly to episodic memory processing, whereas the fifth functional gradient describes a piriform-isocortical pattern related most to olfaction. The authors interpret their findings in the context of the ‘dual origin’ theory ([Sanides, 1962](#)), which posits that cortical evolution emanated along progressive rings of laminar differentiation from origins in the piriform and parahippocampal cortex. Taking a cortex-wide perspective on the interplay between microstructure, connectivity, and hierarchical organization, [Vezoli et al. \(2021\)](#) review laminar-specific projection patterns and their association to cortical hierarchies. Their findings provide evidence for a dual counter stream architecture, which incorporates distance-dependent feedback and feedforward pathways through supra- and infragranular layers, respectively.

Despite a focus of prior work on cortical organization, several studies in the special issue also investigate subcortical structures as well as white matter architecture, which are thought to be key aspects to fully understand whole brain organization and dynamics ([Shine et al., 2019a, 2019b](#)). [Yang et al. \(2020\)](#) derived thalamic functional gradients based on resting-state fMRI, identifying a first medio-lateral and a second anterior-posterior gradient. They furthermore show that the first gradient reflects known thalamic subnuclear divisions, while the second gradient was found to relate to established associations between the thalamus and cortical intrinsic functional communities as well as cognitive ontologies. Also studying thalamic subregional organization and its link to cortex-wide function, [Muller et al. \(2020\)](#) show that different neuronal subpopulations of the thalamus differentially relate to cortical gradients, time scales, and dynamics. They show that *core* neuronal populations (expressing parvalbumin) innervate more strongly granular cortical layers and project more closely to sensory/unimodal regions, while *matrix* populations (expressing calbindin) innervate supragranular layers more diffusely and correlate more closely to higher/transmodal regions with longer time scales. [Cona et al. \(2021\)](#) carry out a meta-analysis of neuroimaging studies that investigates cortical representations for space and time. They identify a set of distributed regions, in-

cluding insular, pre-SMA, opercular and intraparietal regions, and observe a gradient of activation values related to time vs space processing. Assessing interactions between cortical functional organization and white matter architecture, [Friedrich et al. \(2020\)](#) map the principal sensory-transmodal functional gradient to the midsection of the corpus callosum, a major pathway connecting both cortical hemispheres. Transmodal gradient values are found to be represented on the genu, the anterior part of the callosum, while sensory and motor regions are represented more posteriorly, suggesting a potentially mirrored topography of cortical function and inter-hemispheric structural connectivity.

2.2. A coordinate system to understand brain dynamics and cognitive hierarchies

The challenge of linking features of brain organization across scales is crucial for a mechanistic account of brain dynamics and their relation to behavior. Following up on initial findings that the functional as well as microstructural gradients ([Paquola et al., 2019b](#); [Huntenburg et al., 2017](#)) may tap into primate cortical hierarchies ([Mesulam, 1998](#)) and time-varying neural architecture ([Chaudhuri et al., 2015](#); [Gao et al., 2020](#)), several studies in the Special Issue examine the continuous features underlying functional dynamics and cognitive hierarchies.

[Yousefi and Keilholz \(2021\)](#) utilize dynamic rs-fMRI analysis to demonstrate how intrinsic functional activity propagates along macroscale functional gradients, suggesting that these axes may play a role in constraining functional dynamics. [Park et al. \(2021c\)](#) derive cortex-wide structural connectivity gradients from diffusion MRI tractography, and show associations to dynamic functional transitions estimated from resting-state fMRI via hidden Markov models. Notably, structural gradient information helps explaining transitions between sensorimotor states and between sensorimotor and transmodal states, but not between transmodal states. Also aiming at predicting functional dynamics from neurostructural features, [Liu et al. \(2020\)](#) conduct a transcriptome-connectome association study. Leveraging a multivariate approach, the authors show that transcriptional profiles explain approximately 28% of the variation in this spatial layout of functional network dynamics. [Mitra et al. \(2020\)](#) propose a framework for computing probabilistic flow in brain activity and demonstrate how flow probabilities change across rest as well as task states. They furthermore demonstrate that their probabilistic perspective captures both intra- and inter-network dynamics.

In addition to the emerging consensus that gradients may represent important patterns of intrinsic brain organization, it remains to be investigated how far these patterns constrain state-to-state variation in brain function. In several studies, the axes described by functional gradients are used to describe task-evoked patterns of activations and deactivations. Investigating the link between intrinsic neural function and task-evoked activity, [Ito et al. \(2020\)](#) show that across multiple tasks, the magnitude of regional task-evoked activity is high in unimodal areas, but low in transmodal areas. In contrast, task-state functional connectivity is significantly reduced in unimodal areas relative to transmodal areas. Also pointing to hierarchy-dependent shifts in localized vs distributed processing, the negative relationship between localized task activity and distributed connectivity is associated with the principal gradient of macroscale function. [Viviani et al. \(2020\)](#) assess brain gradients of functional activation and deactivation in association cortices during a social decision-making task. The authors identify two distinct networks were differentially recruited, depending on whether the social decision making was informed by sensory vs contextual cues. Notably, these distinct networks are centered at the junction of externally- and internally oriented systems, such as the default mode network. Two studies from the same group further contribute to the notion that the principal functional gradient may capture the spatial layout of networks implicated in higher order and semantic processing. In [Lanzoni et al. \(2020\)](#), the authors study semantic cue integration using task fMRI. They observe max-

imal activation for the convergent cue condition at the heteromodal default mode end of the principal gradients. These findings suggest that the default mode network as being the apex of the sensory-transmodal hierarchy supports states of information integration that constrain ongoing cognition. [Wang et al. \(2020\)](#) contextualize task-fMRI patterns during a semantic judgment task and demonstrate the strongest response when input overlapped with long-term memory, particularly at the transmodal apex. These findings furthermore provide support that the cortical hierarchy captured by the principal functional gradient may serve as an organizational axis of controlled semantic cognition.

Given the ability to characterize ongoing function, a further step is to investigate associations with complex internal states. [McKeown et al. \(2020\)](#) combine experience sampling techniques with resting-state fMRI connectivity gradient analyses and show inter-individual differences in patterns of ongoing thought related to subtle shifts in macroscale gradient organization during wakeful rest. Looking at state-dependent functional changes, [Cross et al. \(2021\)](#) assess functional connectivity gradients derived from fMRI measures during cognitive tasks in individuals after either a normal night of sleep, after 24 h of sleep deprivation, or after a morning recovery nap. Despite finding evidence for state-dependent changes in overall functional connectivity strength, the authors identify relatively consistent functional gradients, suggesting that main axes of functional organization may be relatively preserved across different vigilance states.

2.3. A framework to conceptualize brain evolution and lifespan changes

A rising body of empirical and theoretical papers, as well as the associations between macroscale gradients and underlying molecular factors ([Buckner and Krienen, 2013](#); [Goulas et al., 2019a, 2019b, 2019c](#); [Huntenburg et al., 2018](#); [Valk et al., 2020](#)), suggests that gradients may potentially also serve as important axes of human brain evolution, development, and plasticity.

Contributing to this literature, several papers in the Special Issue leverage gradients to address neural organization across species. [Xu et al. \(2020\)](#) use functional gradients as features to improve cross-species alignment between humans and macaques. Based on this novel alignment approach, they define a functional homology index that correlates with the sensory-transmodal hierarchical gradient in humans, suggesting that transmodal systems such as the default mode network have undergone marked adaptations in recent primate evolution. In [Huntenburg et al. \(2021\)](#), the authors show that the principal gradient of functional connectivity in the mouse cortex recapitulates the axis of neocortical evolution from archicortex and paleocortex described in the dual-origin model. Additional gradients are also reported that reflect sensory specialization and sensory-to-transmodal hierarchy, which serve as second and first gradients in humans. In addition to demonstrating stability of their gradient findings across individuals, the authors observe a correspondence with gene expression patterns. [Lau et al. \(2021\)](#) investigate gene expression gradients in mouse cortex across seven developmental time points, and show that gene expression similarity exponentially decays with physical distance across all developmental time points. Moreover, they find a power law scaling relationship with a linear dimension of brain size, suggesting that the mouse brain achieves a characteristic balance between local molecular similarity and longer-range connective diversity.

Studying human childhood development, [Ball et al. \(2020\)](#) show a correlation between gradual patterns of age-related cortical thinning and cortical gene expression patterns. Reported genes were significantly enriched for neurons, synaptic remodeling, and common cognitive and neurodevelopmental disorders. Taking a lifespan perspective, [Bethlehem et al. \(2020\)](#) study age-related changes in functional gradients, showing an increasing dispersion in frontoparietal, attention and default mode networks, which is furthermore found to be negatively associated with markers of fluid intelligence.

2.4. Conclusions, open questions, and outlook

The study of gradients has become an increasingly established perspective in the neuroscience and network neuroscience communities. Fueled by an increasing array of methodological advances to derive, align, and analyze gradients, this emerging field offers to address fundamental principles of cortical organization, to study structure-function-cognition links, and to examine cortical development and evolution. As for other fields, numerous open questions and issues remain, however, which we anticipate being further addressed in the years to come.

Firstly, a flipside of the proliferation of methods for gradient mapping and alignment might be variability in methodological approaches across the different studies. While prior studies have demonstrated relatively high correspondence of findings across different parameter combinations (Hong et al., 2020; Paquola et al., 2019b), future work is still needed to carefully assess reproducibility and reliability for the different gradients commonly being derived in the field. This research will furthermore answer important questions on the meaning of gradient ordering, and the association between gradient ordering and sensitivity to inter-individual variation.

Gradients offer a framework for the analysis of structure-function correspondence, and there seems to be a high degree of convergence of gradients across different modalities (Sydnor et al., 2021; Paquola et al., 2019b). Yet, there also seem to be some noticeable differences in the gradients that are derived across modalities. For instance, gradients of cortical microstructure more clearly differentiate sensory/motor areas with marked laminar differentiation from paralimbic components of transmodal cortex with only little laminar differentiation, while functional gradients seem to differentiate sensory/motor systems more markedly from the more heteromodal/default mode end of the sensory-transmodal hierarchy. The biological significance of these differences, beyond simple method-related variations, will be an important topic of future research.

The overall correspondence between both functional and microstructural gradients and models of primate cortical hierarchical organization renders gradient approaches appealing for interrogating cognitive architectures. However, in addition to the need for a further nuanced concept of cortical 'hierarchy' per se (Hilgetag and Goulas, 2020), there is an increased need for experimental work assessing the associations between gradient organization and feedforward as well as feedback processing mechanisms in humans and non-human animals (Gonzalez-Garcia and He, 2021; Hardstone et al., 2021).

Cross-species comparative research to date demonstrates the similarity of gradients in other species, alongside notable inter-species differences, supporting the exciting notion that gradients may describe blueprints to understand cortical evolution, development, and plasticity. In future work, systematic comparisons of structural and functional gradients across a wider range of species will be an important step towards the formulation of different evolutionary theory, a research goal which is likely to become increasingly feasible with growing availability of open multispecies *in vivo* datasets (Messinger et al., 2021; Milham et al., 2018). Similarly, studies have begun to chart gradient reconfigurations across the lifespan (Sydnor et al., 2021), and to assess gradient changes as a result of environmental and disease related factors (Valk et al., 2021a). These perspectives will provide important insight into the invariance, as well as malleability of cortical gradients.

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Further reading

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