



Mechanistic versus descriptive interpretation of brain activity pattern reconstruction

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The geometric eigenmodes, derived from the shape of the cortical surface, have been suggested as a better model for explaining brain function due to their high accuracy in reconstructing patterns of both spontaneous and stimulus-evoked brain activity patterns captured by functional MRI, when contrasted with alternative models including structural connectome derived bases. While a descriptive representation offers valuable utility for neuroimaging studies, it is necessary to examine the extent to which it supports a mechanistic explanation for human brain function. Although the observation that geometric eigenmodes accurately fit brain activity is intriguing, we argue that accepting them as a model of brain function risks conflating descriptive and mechanistic interpretations. While a representation that effectively describes the underlying geometry is inherently adept at fitting patterns within that geometric space; it does not necessarily shed light on mechanisms that give rise to the brain's functional attributes. To this end, we provide two lines of empirical results: a) geometric eigenmodes demonstrate a high flexibility when fit to a range of manipulated patterns, and b) localized parcel-based representations can reconstruct activity patterns as well. Based on those results, theoretical considerations, and previous data, we argue that more consideration is needed regarding the complementary roles of descriptive representation and mechanistic explanation in neuroimaging research. While we recognize the potential role of the brain's geometry in influencing its dynamics, assertions regarding its efficacy should be weighed against its inherent lack of specificity, biological interpretability, and anatomical evidence.

brain geometry | mechanistic explanation | neuroimaging methodology | biological interpretability | brain activity reconstruction

Understanding macroscale brain dynamics is a critical objective in neuroscience, as it can provide insights into how large-scale neural systems coordinate to support complex cognitive processes such as perception, memory, and decision-making (1). These dynamics serve as a bridge between microscopic cellular activities and observable behaviors, enabling a more comprehensive understanding of brain function (2). Furthermore, disruptions in macroscale activity patterns are often implicated in neurological and psychiatric disorders, highlighting their clinical relevance (3, 4). Characterizing these dynamics and mechanistic insights into how they come about could facilitate the development of improved diagnostic tools and targeted therapeutic interventions as well as technological advancements like brain–computer interfaces. As such, a robust understanding of macroscale brain dynamics is foundational for both theoretical and applied neuroscience.

There exist several descriptive methods for representing brain activity measured using MRI, including independent component analysis (ICA) (5), functional gradients (6), and clustering of brain regions (7). These methods can reveal organizational patterns in neuroimaging data and can be interpreted in light of biological constraints. However, such patterns do not *by themselves* imply biological organization or provide mechanistic explanation, and the descriptive and mechanistic approaches are often conflated. Subsequently, the identified representations were contextualized with respect to their putative neuroscientific and biological meaning. For example, ICA applied to functional MRI assigns voxels exhibiting similar activity patterns to components, followed by functional interpretation of each component guided and constrained by prior literature, including studies that provide biological or mechanistic evidence. This distinction is not unique to neuroimaging research. An acoustic signal, for instance, can be reconstructed as a combination of bases with different frequencies using the Fourier transform, yet interpreting spectral components in terms of underlying physiological mechanisms requires a causal link between vocal physiology and acoustics (8). This is because the Fourier transform is a descriptive method, and each frequency component does not in itself contain information regarding the physical mechanism producing the acoustic signal (9). Consequently, we emphasize

Significance

Does accurate reconstruction of brain activity imply a biological mechanism? Geometric eigenmodes are proposed as a foundational basis for brain function due to their strong reconstruction performance. We revisit this assumption by distinguishing descriptive utility from mechanistic explanation. We show that their success reflects intrinsic mathematical flexibility, enabling them to fit even nonbiological patterns, while established functional parcellations achieve comparable performance. Rather than dismissing the geometric framework, we highlight the risks of conflating fit with mechanism and call for cumulative verification through collaborative research. By clarifying these interpretive boundaries, this work transforms the geometric framework into a more meaningful tool, fostering the development of truly interpretable and biologically grounded models of brain activity and function.

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that descriptive representations and mechanistic explanations should be clearly distinguished in their utility and applied accordingly in scientific investigation.

Recent advances in neuroimaging research have sought to explain macroscale brain dynamics through novel frameworks, one of which is the geometric eigenmodes (10). Geometric eigenmodes arise from a simplified formulation of neural field theory (NFT). Under the assumptions of homogeneous local interactions and isotropic wave propagation, the NFT equations reduce to a wave equation on the cortical surface whose standing-wave solutions are the eigenfunctions of the Laplace–Beltrami operator (10, 11). These geometric eigenmodes are the natural spatial harmonic modes determined solely by the cortical geometry and boundary conditions without explicitly modeling heterogeneous anatomical connectivity. When compared to alternative models, including eigenmodes of structural connectome and an exponential distance rule (EDR), geometric eigenmodes demonstrate superior performance in fitting patterns of spontaneous and stimulus-evoked brain activity patterns. Based on those observations, the geometric eigenmodes approach was proposed as providing a more parsimonious and accurate mechanistic account of task-related fMRI activity. More specifically, the high accuracy of the geometric eigenmodes in reconstructing cortical activity patterns compared to alternative eigenmode bases was interpreted as evidence that wave dynamics constrained by cortical geometry primarily govern large-scale brain organization. This interpretation challenges the traditional view that brain function is shaped by anatomical white matter connectivity, exemplified by the role of the arcuate fasciculus in linking Wernicke's and Broca's areas during language processing (12).

Those claims have generated a healthy discussion within the community regarding the role of brain geometry in its function. Critiques have emerged that emphasize the limitations of geometric eigenmodes in capturing the full complexity of macroscale brain dynamics, advocating for a greater focus on structural connectivity. A recent opinion suggests that integrating structural connectivity with other modeling approaches provides a more comprehensive framework for understanding brain function, particularly in explaining dynamic interactions across distributed structural information encompassing connectivity, geometry, and microstructures (13). Complementing these arguments, another study highlights that while geometric eigenmodes effectively model cortical geometry, they neglect the critical influence of anatomical connections, which are central to brain network organization and function (14). Similarly, the importance of long-range structural connectivity in shaping neural activity patterns has been underscored, which geometric models alone fail to adequately capture (15). Furthermore, it can inadvertently be overlooked as topologically complex and long-distance white matter connectivity, beyond what can be captured by a nonspecific EDR (16). Together, these perspectives position geometric eigenmodes as a particularly striking example of a broader question: To what extent does a strong model fit provide biological insight, given that high reconstruction accuracy alone does not necessarily imply a mechanistic explanation? Specifically, a mechanistic interpretation requires that the superior reconstruction performance of geometric eigenmodes be preferentially associated with biologically meaningful cortical patterns, rather than arising from a more general capacity to represent spatial structure. Consequently, the spatial specificity of the reconstruction framework warrants rigorous evaluation.

To this end, we performed empirical experiments to reconstruct biological and nonbiological (unrelated to brain function) patterns using several bases. In addition to the eigenmodes used by Pang

et al. (10), we included bases derived from parcel-based representations emphasizing localized structures which also showed accurate reconstruction. This choice reflects the longstanding influence of regional specialization in neuroimaging supported by converging evidence across multiple methodological traditions including both histological and functional mapping. Our results demonstrate the high flexibility of geometric eigenmodes in reconstructing manipulated and artificial spatial maps, indicating a lack of specificity for neurobiologically meaningful patterns. This apparent success of geometric eigenmodes may reflect their inherent alignment with the geometric structure of the brain (as the patterns are indeed projected on the same geometrical shape), rather than revealing underlying functional mechanisms, raising concerns about the explanatory power of such models. Together with theoretical considerations and existing data, these results underscore the need to critically evaluate the parsimony, robustness, and generality of geometric eigenmodes as a model of brain function.

Overall, we consider geometric eigenmodes a descriptive representation with substantial value for data description and compression. Importantly, success in these goals should not be conflated with characterization or mechanistic explanation of the underlying neural system. Accordingly, broader claims require converging evidence and dedicated explanatory investigation. In this view, descriptive representations are not endpoints but starting points to understand and explain the biological system. While the role of cortical geometry in shaping brain dynamics is undeniable, its efficacy as an explanatory model must be weighed against simpler alternatives, its potential lack of specificity, and anatomical evidence. Thus, we argue that interpreting geometric eigenmodes as a mechanistic model for brain function risks oversimplifying the complexities of neural dynamics.

Results

Brief Overview. The primary purpose of this work was to examine the interpretation of geometric eigenmodes in brain activity reconstruction. To do this, we reconstructed nonbiological and randomized brain activity patterns using several bases, including geometric and connectome eigenmodes, and newly proposed Parcel and Parcel+Connectome modes. Spatially localized Parcel bases were constructed from Schaefer parcellations of corresponding granularity, with each parcel represented as a distinct spatial basis. Parcel+Connectome bases additionally retain information regarding distant connections by incorporating structural connectivity between the corresponding parcels (*Methods* and *SI Appendix, Fig. S1*). Following Pang et al. (10), reconstruction was performed at the vertex level (32,492 vertices, left hemisphere), while reconstruction accuracy was quantified as the Pearson correlation between parcel averaged (180 left hemispheric parcels of the Glasser 360 parcellation) values of the original and reconstructed maps (*Methods*). We report vertex-level accuracy where appropriate.

Briefly, we show that geometric eigenmodes reconstruct nonbiological patterns with high accuracy, including images projected onto the cortex and randomized brain activity maps. For the latter, manipulated patterns are in some cases reconstructed even more accurately than the corresponding empirical brain activity patterns. We further identify many-to-many associations in which spatially dissimilar or even anticorrelated activity patterns can rely on similar combinations of geometric eigenmodes. Finally, we show that eigenmodes with high reconstruction performance tend to distribute their representational capacity more uniformly across the cortex. Taken together, these findings indicate that the high reconstruction fidelity of geometric eigenmodes extends across a

broad range of spatial patterns and is not specific to biologically meaningful activity patterns, positioning reconstruction primarily as a measure of descriptive capacity rather than mechanistic specificity.

Are Geometric Eigenmodes Only Good at Reconstructing Feasible Brain Activity Patterns? The notion that the brain function is intricately linked with the geometry of the cortex is a highly compelling one, given that patterns of brain activity can be almost perfectly represented by a set of geometric eigenmodes of the cortex (10). However, it is also possible that the geometric eigenmodes can reconstruct patterns entirely unrelated to brain activity. To test this, we employed geometric eigenmodes to reconstruct six nonbiological patterns from drawings and photographs projected on the cortical surface.

These patterns were reconstructed with remarkable accuracy using geometric eigenmodes (Fig. 1 *A* and *B*). We subsequently calculated reconstruction accuracy across varied numbers of modes derived from different schemes including geometric, Parcel, and Parcel+Connectome and compared their accuracies while using 50, 100, and 200 modes (Fig. 1 *C*). Reconstruction of nonbiological patterns using other bases had lower accuracies compared to geometric eigenmodes (see *SI Appendix, Fig. S2* for vertex-level accuracies).

The pictures had different statistical properties than the 47 activation patterns. Parcel-level Pearson's correlation between the pictures and activation patterns were rather low (282 pairs; mean = -0.12 and SD = 0.22). In addition, the estimated smoothness (full-width-half-maximum) of five pictures (except Cat) were significantly different from the activation patterns (mean = 5.44 and SD = 0.49 , *SI Appendix, Fig. S3*). To further increase distinctiveness, we removed the variance explained by the 47 task activation maps from the pictures. The residuals were reconstructed accurately (mean = 0.96 and SD = 0.02 ; *SI Appendix, Fig. S4*).

Limited Functional Constraints Are Reflected in a Lack of Specificity of Geometric Eigenmodes. Using the 47 HCP task activation maps, we tested the specificity of the geometric eigenmodes comparing it with other eigenmodes and Parcel and Parcel+Connectome bases at different granularities (Fig. 2*A*). The geometric eigenmodes showed the highest accuracy when 200 eigenmodes were used, which was significantly higher ($P < 0.05$, two-sided t test, Bonferroni corrected) and stronger effect sizes (Cohen's d) than the second highest accuracy shown by Parcel+Connectome (Fig. 2*A*, 200 modes). Interestingly, the Parcel+Connectome basis showed a better reconstruction than

geometric eigenmodes when using 100 bases and significantly so at 50 bases (Fig. 2*A*; 100 and 50 modes, yellow bars). This result demonstrates that, under certain contexts, geometric eigenmodes are not uniquely optimal for capturing the spatial structure of the observed cortical patterns. As a robustness check, we compared reconstruction using the Schaefer parcellation with a cortical parcellation derived from geodesic distances, which is expected to contain less biologically informed regional structure. The Schaefer parcellation generally achieved higher reconstruction accuracy, supporting its use as the biologically grounded parcel-based representation in our main analyses (*SI Appendix, Supporting Information 1*).

We next performed reconstruction of randomized brain activity patterns to probe the limits of functional constraints. A high accuracy here would indicate a high capacity to reconstruct any pattern and hence a lower likelihood of representing functional constraints. To this end, we utilized 200 bases from geometric eigenmodes, Parcel, and Parcel+Connectome bases to reconstruct seven key HCP task-contrast maps and their spin randomized versions ($N = 5,000$) (17). When reconstructing original maps, the accuracy of geometric eigenmodes was higher with strong effect sizes (Fig. 2*B*; bar plots). For each basis, the randomized-map comparisons were categorized as showing either specificity, when randomized maps were reconstructed with significantly lower accuracy than the original brain activity pattern, or a lack of specificity, when randomized maps were reconstructed with significantly higher accuracy than the original pattern. Geometric eigenmodes exhibited a lack of specificity in all tasks except for gambling, while Parcel+Connectome demonstrated a lack of specificity only for the emotion task (Fig. 2*B*, green lines). In a similar analysis using an alternative randomization method [Moran's method (18)], the geometric eigenmodes exhibited a lack of specificity in four tasks (emotion, motor, relational, and social), while the Parcel+Connectome basis again showed a higher accuracy for randomized patterns only in the emotion task (*SI Appendix, Fig. S5*).

To further investigate, in addition to the reconstruction accuracy, we sought to ascertain the numerical contribution of the geometric eigenmodes to the reconstruction process. The objective was to test the proposition that geometric eigenmodes constitute a fundamental basis for describing brain functional activity. If this is the case, reconstruction of similar activity patterns should be based on similar contributions from the individual eigenmodes. We quantified these contributions using the beta coefficients obtained from the multiple linear regression during reconstruction. Accordingly, for each rotated pattern ($N = 5,000$), we assessed both the similarity between the original and rotated spatial

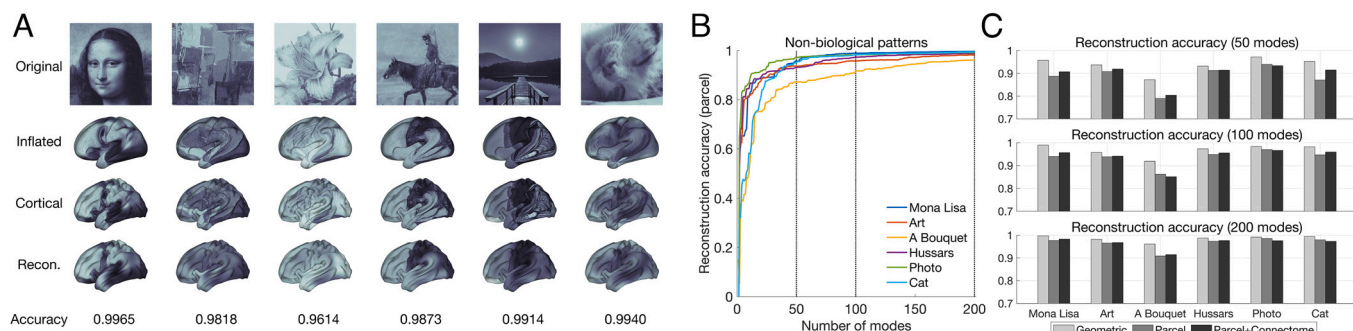


Fig. 1. Reconstruction to nonbiological brain patterns. (*A*) Nonbiological patterns of six pictures projected on the cortical surface and corresponding reconstructed patterns using 200 geometric eigenmodes with the parcel-level accuracy between original and reconstructed pictures. Geometric eigenmodes show a high reconstruction accuracy for these nonbiological patterns. (*B*) Parcel-level reconstruction accuracy of the same images for different number of geometric eigenmodes. For all pictures, the reconstruction accuracy increases with the number of modes used as expected. (*C*) Reconstruction accuracies using 50, 100, and 200 modes with different granularities from geometric eigenmodes and Schaefer parcellation derived Parcel and Parcel+Connectome bases.

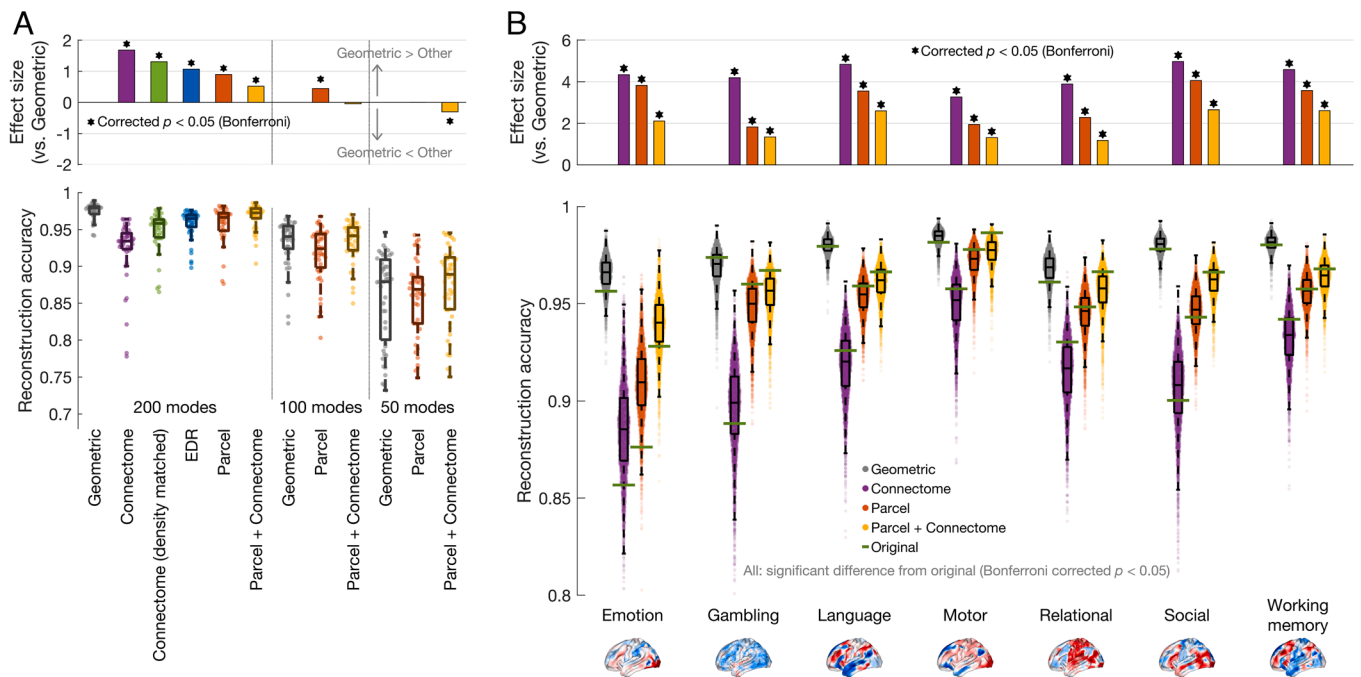


Fig. 2. Reconstruction accuracy using geometric eigenmodes and region-based modes with different spatial granularities. (A) Distributions of reconstruction accuracy of geometric eigenmodes and five other bases in 47 tasks and the corresponding effect sizes (Cohen's d) of difference in accuracies between Geometric eigenmodes and the other bases. For the "Parcel" and "Parcel+Connectome," Schaefer parcellations of 400, 200, and 100 parcels were used for 200, 100, and 50 modes (only the left hemisphere), respectively. Statistical tests for differences against Geometric eigenmodes were performed using two-sided t test and Bonferroni correction for multiple tests (corrected $P < 0.05$). (B) Reconstruction accuracy to 5,000 randomized brain activity patterns in each task. 200 modes were used for each base condition (4 base conditions: Geometric, Connectome, Parcel, and Parcel+Connectome). All pairs of conditions showed significant differences from the reconstruction accuracy of the original brain activity patterns (green lines). Two-sided t tests were applied and Bonferroni corrected P values were calculated. In accordance, effect sizes (Cohen's d) between Geometric eigenmodes and the other 3 base conditions were also calculated in each key task.

patterns and the similarity between their corresponding reconstruction beta-weight profiles. Five of seven key tasks showed the expected relationship, in which spatial pattern similarity was highly positively associated with beta-weight similarity and the relationship crossed the origin (e.g., the relational task; Fig. 3*A* and *SI Appendix*, Fig. S6). Thus, similar patterns were reconstructed using similar eigenmode contributions, whereas dissimilar patterns relied on correspondingly dissimilar contributions. In

contrast, gambling and motor tasks did not show this behavior: The correspondence was weaker and beta-weight correlations remained predominantly positive even for rotated maps that were negatively correlated with the original map. Thus, spatially dissimilar or even anticorrelated patterns could be reconstructed using similar eigenmode contributions. These absent or many-to-many associations challenge the assumption that geometric eigenmodes constitute a fundamental basis for characterizing

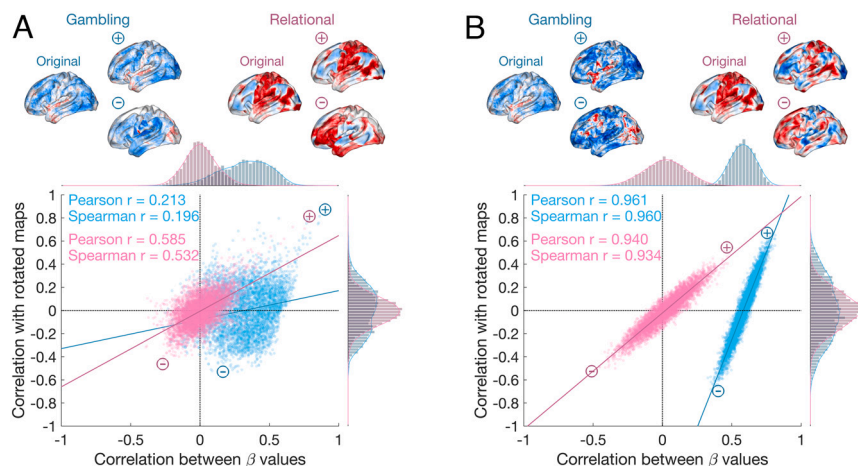


Fig. 3. Reconstruction of randomized brain activity maps and weights of geometric eigenmodes. (A) Correlation between regression weights (beta values) obtained for reconstruction of original and rotated activity maps using 200 geometric eigenmodes (horizontal axis), and correlation between the original and rotated maps (vertical axis). Spin permutation was used to obtain the rotated maps ($N = 5,000$). The gambling task (blue) shows mostly positive correlation of beta values while correlations between maps are distributed around zero. On the other hand, the relational task (red) shows distributions around zero for both correlations. The maximum (positive) and minimum (negative) correlations of maps are indicated with "+" and "-", respectively, and their maps are shown above. (B) A similar analysis using Moran randomization, which shows a similar tendency of distributions as in the panel A. As Moran randomization better preserves the spectral properties of the image, the obtained correlations are higher.

patterns associated with brain function. To support this assertion, we obtained patterns using Moran randomization, which yielded consistent outcomes (Fig. 3B and SI Appendix, Fig. S7). These results complement the demonstration by Faskowitz et al. that geometric eigenmodes derived from nonbrain meshes also reconstruct brain activity patterns (16).

Evenly Distributed Basis Patterns Facilitate Better Reconstruction. To interpret reconstruction accuracy, which is an outcome of a fitting exercise without conflating it with mechanistic explanation, it is important to consider the representational capacity of the bases, i.e., how the retained eigenmodes represent the cortical space. Eigenmodes are ordered from low to high spatial frequency. For instance, the first geometric eigenmode encompasses the entire hemisphere with subsequent eigenmodes capturing higher spatial frequency. Consequently, increasing the number of eigenmodes increases the degrees of freedom and can improve reconstruction of more complex patterns, indicating performance gains due to the representational capacity.

To examine the distribution of the representational capacity of the subspaces spanned by 200 eigenmodes, we calculated vertex-wise statistical leverage at each cortical location (Fig. 4). As the total leverage is fixed to the number of modes, differences between bases reflect how this fixed representational capacity is distributed across the cortical surface. Geometric eigenmodes showed highly uniform spatial coverage (coefficient of variation, $CV = 0.33$), similar only to the refined Connectome SM

eigenmodes ($CV = 0.32$), and substantially more uniform than EDR, Connectome (derived from a sparse, heterogeneous connectivity graph), and density matched Connectome ($CV = 0.64$, 1.05 , and 2.23 , respectively) (Fig. 4A–E). The rank-ordered parcel-wise leverage distributions further illustrated this difference: Geometric and Connectome SM eigenmodes showed comparatively flat profiles, whereas the other bases exhibited steeper declines, indicating greater concentration of representational capacity in a subset of cortical locations (Fig. 4F). We additionally quantified the spatial distribution of reconstruction residuals, defined for each vertex from the discrepancy between its original and reconstructed values across the 47 task maps. These residuals were relatively uniformly distributed for geometric eigenmodes ($CV = 1.40$), similar to EDR ($CV = 1.39$) and Connectome SM eigenmodes ($CV = 1.43$), and more uniform than for Connectome (density matched) ($CV = 1.55$) and particularly Connectome ($CV = 2.05$).

We then correlated redundancy (1-leverage) with mean squared reconstruction residuals averaged across the 47 tasks. A positive correlation indicates that cortical locations with lower representational capacity tend to exhibit larger reconstruction errors. Although leverage is a useful indicator of this association, it does not fully determine reconstruction performance as it captures only local representation and ignores interactions across cortical locations. Geometric eigenmodes showed a weaker association between redundancy and reconstruction error than Connectome eigenmodes (Fig. 4A and B). The density-matched connectome showed

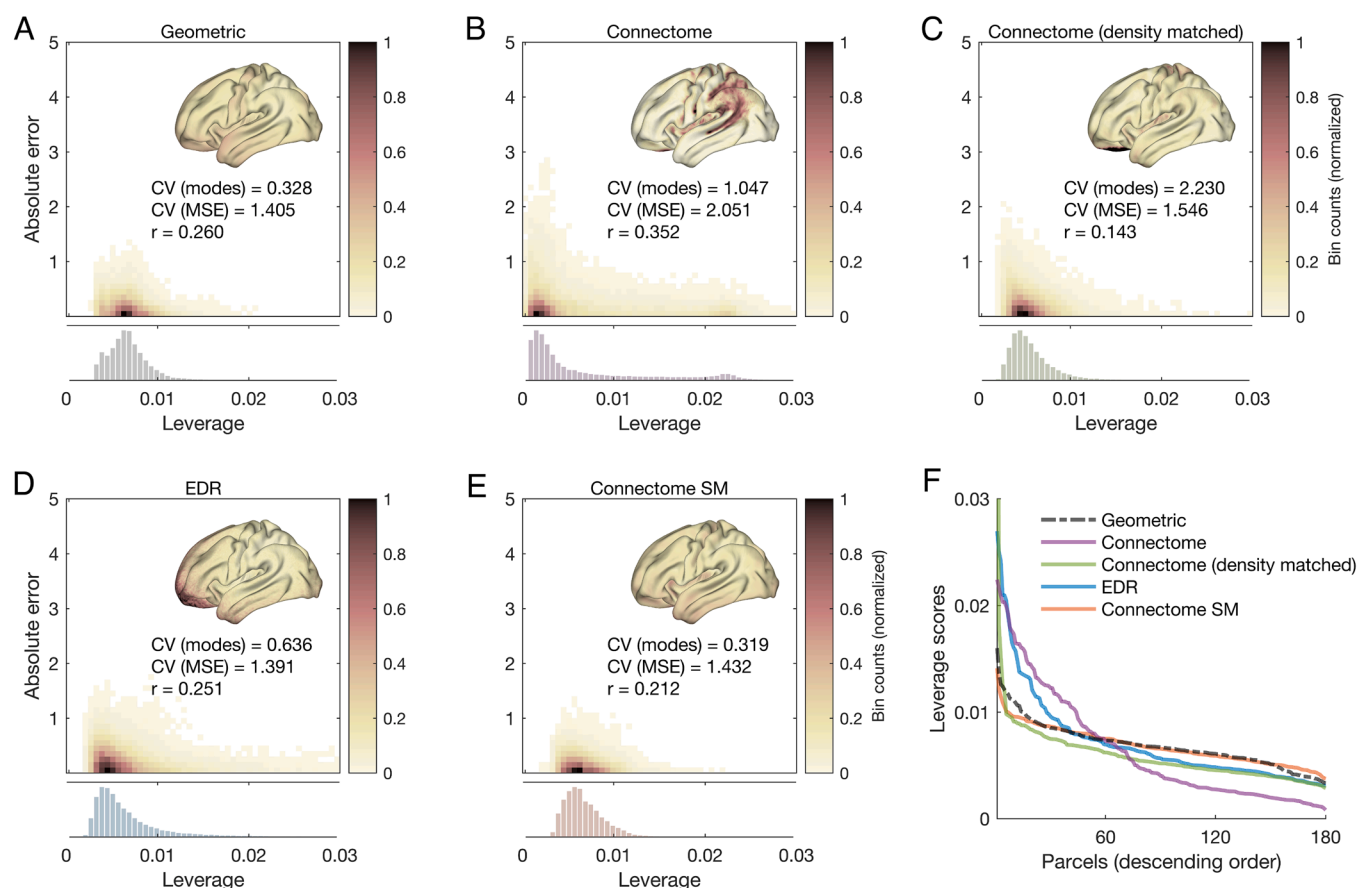


Fig. 4. Distribution of eigenmode representation capacity and reconstruction error. (A–E) Bin maps of leverage scores of eigenmodes and reconstruction error at each vertex in Geometric, Connectome, Connectome (density matched), EDR, and Connectome SM (Sina Mansour et al. (14)). Leverage score maps on the left hemispheric cortical surface of each eigenmode are presented in each panel together with CV of modes and MSE and Pearson correlation between 1-leverage score and MSE using 200 modes of each panel. Note that the colormap for each panel was scaled independently in 0–1 for better visualization. (F) Parcel-level leverage scores in descending order of parcels.

an even weaker association, whereas EDR errors more closely tracked local representational capacity (Fig. 4 C and D). Refined Connectome SM eigenmodes combined relatively uniform representational capacity with a moderate redundancy-error association (Fig. 4E). Together, these findings indicate that reconstruction performance is partly related to how the retained eigenmode subspace represents cortical space, while also depending on interactions across locations. Because cortical images are represented and evaluated on the same surface that defines the geometric eigenmodes, their uniform spatial coverage may facilitate reconstruction of diverse patterns, highlighting a contribution of descriptive capacity to reconstruction accuracy.

Discussion

The aim of this study was to critically assess the scientific validity of the proposition that the geometric structure of the cerebral cortex constrains brain function (10). We acknowledge that the morphology of components in biological systems can impose constraints on their functions. However, often a single structural feature is unlikely to sufficiently account for the full complexity of the system's behavior. In highly intricate systems such as the human brain, where diverse components interact across multiple spatial and temporal scales (19, 20), it is unlikely that cognitive functions can be comprehensively understood through a single aperture.

Pang et al. showed that linear combinations of geometric eigenmodes derived from the Laplace–Beltrami transform of the cortical shape achieve high accuracy in reconstructing brain activity patterns. As geometric eigenmodes correspond to standing-wave solutions of NFT under simplifying assumptions of spatially homogeneous local interactions and isotropic propagation, their high reconstruction accuracy was interpreted as evidence that cortical geometry fundamentally constrains brain function. Supporting this interpretation would require demonstrating that spatial patterns unlikely to occur in empirical brain activity are correspondingly poorly reconstructed by geometric eigenmodes. Therefore, we investigated whether there exist patterns that cannot be reconstructed by linear combinations of geometric eigenmodes. Our findings indicate that geometric eigenmodes faithfully reconstruct synthetic and manipulated patterns unrelated to brain function (Figs. 1–3). These results suggest that geometric eigenmodes constitute a general spatial basis set capable of approximating a broad range of spatial patterns within a given resolution. This is a general property of basis expansions, which can span a representation space analogously to the Fourier bases for temporal or spatial signals. Reconstruction of activity patterns measures descriptive capacity rather than causal influence and claims of biologically *relevant constraints* require converging evidence and mechanistically interpretable, falsifiable predictions.

In their preprint, Faskowitz et al. showed that spatially rotated activity maps can be reconstructed with accuracy comparable to empirical maps (16). In response, Pang et al. argued that spin-based nulls are imperfect for evaluating geometric eigenmodes because projecting cortical data onto a sphere distorts cortical geometry, causing the eigenmodes to approach spherical harmonics in the degenerate limit. Under spherical rotation, coefficient weights can be redistributed among modes within degenerate eigengroups while preserving their overall power, allowing reconstruction accuracy to remain similar despite changes in individual mode contributions (21). However, there is no perfect spatial null, as different methods preserve different properties of the empirical map. BrainSMASH-based surrogates (22) were proposed as an alternative to spin tests (21), but

BrainSMASH does not preserve the full spatial power spectrum of the original map (23). As geometric-eigenmode reconstruction depends strongly on power across spatial wavelengths, such nulls may therefore be expected to show lower reconstruction accuracy simply because their spectral composition might change, limiting the inference that can be drawn from this difference. The choice of spatial null therefore remains under debate, and further work is needed to determine which nulls are most appropriate for assessing biological specificity. These considerations qualify what can be inferred from spin tests but do not eliminate their relevance to biological specificity. If high reconstruction accuracy reflects constraints imposed by cortical geometry on the observed organization of brain activity, empirical activity patterns should be preferentially reconstructed relative to alternative spatial arrangements that retain similar generic spatial properties but alter their correspondence with cortical anatomy. Spin-based as well as Moran randomization nulls provide an approximate test of this expectation by relocating the activity pattern while broadly preserving its spatial structure. Comparable reconstruction of the rotated patterns therefore indicates that reconstruction accuracy alone does not distinguish the observed biological topography from alternative spatial arrangements. In addition, our beta-profile analysis shows that spatially dissimilar or even anticorrelated patterns can rely on similar contributions from individual geometric eigenmodes, further demonstrating a nonunique relationship between cortical topography and its geometric eigenmode representation.

As a marked contrast to the globally distributed eigenmodes, we also evaluated reconstruction using localized parcel-based representations, both alone and combined with structural connectivity (Fig. 2). These representations generally showed lower reconstruction performance than geometric eigenmodes. Comparison of reconstruction of observed brain activity patterns and their randomly altered versions revealed a lack of specificity of geometric eigenmodes, which often reconstructed randomized data better than empirical activity patterns. In contrast, the localized bases showed relatively better specificity to the empirical patterns. This lack of specificity weakens the interpretation that high reconstruction accuracy reflects constraints imposed by cortical geometry.

The correspondence between spatial-map similarity and the associated eigenmode beta profiles provides an additional test of whether geometric eigenmodes constitute a consistent functional representation (Fig. 3). Although several tasks showed the expected correspondence, two tasks exhibited positively correlated beta profiles for spatially dissimilar or even anticorrelated patterns. Such many-to-many associations indicate that reconstruction of distinct patterns can rely on similar combinations of geometric eigenmodes, i.e., reconstruction itself is not uniquely determined.

We also showed that reconstruction accuracy is influenced by how effectively its retained subspace distributes representational capacity across cortical space (Fig. 4). This more uniform representation does not make geometric eigenmodes intrinsically more valid; rather, it reduces spatially underrepresented regions within the truncated basis, potentially contributing to more consistent reconstruction across the cortical surface. In line with this, Sina Mansour et al. showed that improved connectome eigenmodes approached the reconstruction performance of geometric eigenmodes (14). These modes as we show also distribute representational capacity similarly uniformly across the cortex. Thus, part of the reconstruction advantage of particular eigenmode bases may reflect their descriptive properties. Consequently, such numerical comparisons cannot establish whether geometry or

connectivity provides more biologically valid mechanism. Resolving this question requires evidence beyond reconstruction accuracy, particularly evidence linking the respective eigenmodes to neural dynamics or responses to perturbation.

Overall, accurate reconstruction of nonbiological patterns, lack of specificity, and many-to-many associations call into question the interpretation of high reconstruction performance as evidence for a biological mechanism of geometric eigenmodes. Thus, even if *wave dynamics unfolding on the geometry of the cortex* provides a generative mechanism for complex spatiotemporal brain activity, our results indicate that reconstruction accuracy with geometric eigenmodes is not sufficiently selective to support a direct mechanistic attribution. Linking eigenmode reconstruction success with traveling wave mechanisms therefore risks attributing broad descriptive capacity to biological wave dynamics, whereas cortical wave studies aim to isolate biologically grounded dynamical signatures. More generally, the same limitation applies to any particular representation—whether based on geometry, connectivity, or parcellation—as reconstruction performance alone cannot establish that the representation causally constrains brain function.

Rigorous biological interpretation requires cross-corroboration using as different modalities, including neuronal histology (24), neurotransmitter receptor distributions (25), human connectome (26), and neuronal cell types (27), whose relationship to cortical geometry and geometric eigenmodes remains unclear. In contrast, parcellation-based representations of regional biological organization have longstanding support from converging and epistemically direct evidence that links spatial organization to microstructure and function. Invasive primate studies delineated cortical areas using convergent evidence across function, architecture, connectivity, and topographic organization (FACT categories), providing reproducible regional organization and principled constraints on interpretation (28). Focal lesion studies provide complementary evidence by linking localized brain damage to specific functional impairments, thereby further constraining mechanistic interpretation (29). Histological and cytoarchitectonic mapping, including JuBrain, further grounds regional parcellations in directly observed tissue microarchitecture (30). Thus, although parcellations likewise cannot be interpreted as causal mechanisms based on reconstruction performance alone, their biological interpretation is supported by independent evidence across multiple experimental modalities. This distinction becomes particularly relevant across spatial scales: At the nanometer scale accessible via electron microscopy (31), the smooth, continuous cortical meshes lose direct physical correspondence, as neural tissue comprises a complex three-dimensional arrangement of neurons, glia, and their interconnections. Consequently, the reported high reconstruction accuracy of geometric eigenmodes should not by itself be interpreted as evidence for the primacy of geometry over other biological determinants.

From a computational neuroscience viewpoint, a model fit becomes mechanistically meaningful when it is developed under biologically interpretable modeling framework that generates measurable signals and yields testable, ideally falsifiable, predictions. Neural mass and neural field models exemplify this by parameterizing neurobiological processes, for example, effective connectivity (32), excitation–inhibition balance (33), and conduction delays (34). In contrast, support for a functional role of geometric eigenmodes has relied on wave models defined solely by cortical geometry, without explicitly incorporating white-matter axonal connectivity. Their mechanistic interpretation therefore crucially depends on the validity of the assumptions underlying their derivation from NFT, including homogeneous local

interactions and isotropic wave propagation. Their mechanistic interpretation therefore depends critically on the validity of the underlying NFT assumptions, including spatially homogeneous local interactions and isotropic wave propagation, as well as treating an MRI-derived cortical surface mesh as a meaningful substrate for neural dynamics. Whether these assumptions and this anatomical abstraction capture the dominant principles governing large-scale brain dynamics remains to be established. In addition, although the wave-based model was compared with a connectome-based neural mass model, this comparison examined only a particular model and dynamical regime. Neural mass modeling encompasses a broad class of frameworks that can incorporate a range of mathematical or biological features, including local recurrent dynamics (35–37), regional oscillators in delayed coupling (38, 39), and heterogeneous coupling parameters (35, 37). Results also depend on the structural connectome characterization and refined processing addressing streamline density, gyral bias, intensity normalization, bias field correction, and smoothed weighted connectivity, can provide better models (40), as also demonstrated for comparable reconstruction with geometric eigenmodes (14). Current neuroscientific evidence suggests that brain dynamics emerge from the interplay between local propagation of neural activity within cortical gray matter and long-range interactions mediated by white-matter connectivity (41, 42). Models with distinct theoretical foundations may therefore provide complementary insights into the multidimensional mechanisms underlying brain dynamics, with wave-based models offering one plausible perspective among many. In line with this, recent efforts in the development of digital twin brain frameworks (43) emphasize the importance of considering multiscale features of the brain into an integrated system to achieve a holistic understanding of brain function.

Despite these limitations, geometric eigenmodes provide a useful framework for several applications, as demonstrated by recent extensions of the approach. For example, an NFT-based geometric eigenmode model was applied to mammalian brains and outperformed existing approaches in reproducing topological and topographical properties (44). A combination of geometric and connectome eigenmodes were used to model seizure-related brain signals (45). Koussis et al. (23) proposed a method that preserves spatial autocorrelation by decomposing brain maps into geometric eigenmodes and randomly rotating these modes, thereby providing statistically rigorous null models for spatial analyses of brain maps. Furthermore, the Laplace–Beltrami spectrum (i.e., the eigenvalues) of several brain structures has been shown to have a genetic basis (46). These studies demonstrate that the geometric framework provides a useful descriptive and analytical tool across a range of contexts.

Taken together, the geometric eigenmodes represent a meaningful step forward as an advanced approach to model large-scale brain dynamics, one that highlights aspects potentially overlooked in previous models. Nevertheless, robust evidence confirming their mechanistic role is yet to be established. Future work identifying candidate generative bases can build on our framework and the preprint from Faskowitz et al. (16) to assess whether they reconstruct patterns unrelated to brain activity, but establishing their mechanistic relevance will ultimately require experimental validation. Consequently, balancing descriptive capacity and extracting verifiable mechanistic insights is crucial. We thus suggest integrating this approach with complementary models to provide a more complete picture of brain function that incorporates both geometrical constraints and biologically grounded parcellation and connectivity patterns. This discussion also underscores the importance of critically evaluating scientific claims through rigorous logical analysis, supported by collaborative and transparent exchange

among researchers (13–16). We are grateful for the opportunity to engage in such a discussion and hope that continued critical and constructive dialogue will contribute to the development of robust models of brain function.

Methods

The current study used the Human Connectome Project young adult (HCP-YA) dataset (47). The HCP-YA scanning protocol was approved by the local Institutional Review Board at Washington University in St. Louis, and all participants provided written consent before participation. Approval for retrospective analysis was given by the ethics committee at the Faculty of Medicine at Heinrich Heine University Düsseldorf (Study No. 2018-317-RetroDeuA).

Cortical Maps and Reconstruction. To transcribe a pattern completely unrelated to brain activity onto the cerebral cortex, a two-dimensional image or photograph was first mapped onto a spherical surface. This was achieved by converting a polar coordinate system into a spherical coordinate system. The value at each vertex was computed as bilinear interpolation of values around it. The spherical surface pattern was then deformed onto the left hemisphere cortical surface (32,492 vertices) according to the indices of each vertex. The images were obtained on the Internet and available for noncommercial use.

The original brain activity patterns were used as provided by Pang et al. Randomized brain activity patterns were obtained by manipulating the original brain activity patterns ($N = 5,000$) in two different ways, spin permutations and Moran transformation (17, 18) as implemented in the BrainSpace toolbox (48). In addition, to estimate smoothness of cortical patterns, we utilized *mrifwfm* in FreeSurfer for 47 tasks as well as 6 pictures.

Reconstruction and accuracy calculations followed the same procedure as Pang et al. (10). A pattern on the cortical surface was reconstructed at the vertex level using multiple linear regression using a given basis without additional intercept term. Pearson's correlation between the original pattern and reconstructed pattern was calculated as reconstruction accuracy at the parcel level using average values within 180 parcels from the HCP-MMP1 parcellation (the Glasser atlas) (49). That is, reconstruction was performed at the vertex level, and accuracy was calculated at the parcel level. In addition, we also calculated vertex-level accuracy by correlating the values across vertices and report it where appropriate.

Eigenmodes, Parcellation, and Connectome Bases Used for Reconstruction. The geometric, Connectome, Connectome (density matched), and EDR eigenmodes were obtained from Pang et al. (10). The Connectome SM eigenmodes were taken from Sina Mansour et al. (14). The first modes (low spatial frequency) were used when evaluating the effect of increasing number of eigenmodes.

We additionally defined "Parcel" and "Parcel+Connectome" modes. Parcellations were derived using the Schaefer atlas with varying levels of granularity (100, 200, and 400 parcels, only left hemisphere used) (50). The Parcel modes were defined for each parcel as corresponding vertices with values 1 and 0 elsewhere. The Parcel+Connectome additionally incorporated white-matter connectivity (structural connectome from Pang et al.) between corresponding parcels.

Additionally, we obtained parcellation using the k-medoids clustering applied to the geodesic distances between the vertices (calculated using the HCP workbench) at varied granularity (100, 200, 360, and 400 parcels). This parcellation is not expected to carry anatomical or functional information. To assess the similarity between these uniformly partitioned brain maps and the atlases with the same number of regions, we computed the adjusted Rand index (51).

Vertex-Wise Representational Capacity and Reconstruction Error. We quantified the spatial representational capacity of each eigenmode basis as leverage score at each vertex. For each basis, Geometric, Connectome, Connectome (density matched), EDR, and Connectome SM suggested by Sina Mansour et al. (14), we first computed the leverage scores of the truncated basis ϕ with 200 modes. We calculated leverage score l_i at each vertex i through K modes as the diagonal entries of the projection matrix (52):

$$l_i = (P_K)_{ii}; P_K = \Phi_K (\Phi_K^T \Phi_K)^{-1} \Phi_K^T.$$

Reconstruction error (mean squared error, MSE) was calculated for all 47 tasks and averaged to get an empirical estimate of expected error at each vertex using corresponding eigenmodes. This analysis allowed us to compare how different eigenmode bases distribute representational capacity across the cortex and how this localized capacity relates to their ability to accurately reconstruct brain activity patterns.

Statistical Analysis. Group differences were assessed using two-sided two-sample t tests, with Bonferroni correction applied for multiple comparisons where appropriate. Statistical significance was defined as $P < 0.05$. Effect sizes were quantified using Cohen's d , calculated as the difference between group means standardized by the pooled within-group SD. All statistical tests and visualization were performed in MATLAB (R2020b; MathWorks).

Disclosure. Image credits: Mona Lisa, Leonardo da Vinci, Public Domain/Wikimedia Commons; abstract artwork, Steve A Johnson/Pexels; botanical illustration, Unsplash; Hussars, Henri de Toulouse-Lautrec, National Gallery of Art (CCO); landscape photograph, James Wheeler/Pexels; cat photograph, Fabricio Trujillo/Pexels. Generative AI tools were used solely to improve the clarity, grammar, and readability of the manuscript. The authors reviewed and revised all AI-assisted text and take full responsibility for the accuracy, integrity, and final content of the manuscript. No AI tool was used to generate scientific results, analyses, or conclusions.

Data, Materials, and Software Availability. Anonymized GitHub data have been deposited in BrainEigenmodes (10.1038/s41586-023-06098-1) (10). BrainSpace (<https://brainspace.readthedocs.io>) (53) for spin tests. BrainEigenmodes (<https://github.com/NSBLab/BrainEigenmodes>) (54). Adjusted Rand index (https://github.com/cmccomb/rand_index) (55).

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