Novel approaches to functional lateralization: Assessing information in activity patterns across hemispheres and more accurately identifying structural homologues

Marc N. Coutanche[1,2,3], Jake Sauter[4], Essang Akpan[1,2], Rae Buckser[1,2], August Vincent[1,2], & M. Kathleen Caulfield[1]

[1] Department of Psychology, University of Pittsburgh, PA 15260
[2] Learning Research & Development Center, University of Pittsburgh, PA 15260
[3] Brain Institute, University of Pittsburgh, PA 15260
[4] State University of New York at Oswego, Oswego, NY

Corresponding author:

Marc N. Coutanche, Ph.D.
marc.coutanche@pitt.edu
LRDC, Murdoch Building, 525, 3420 Forbes Ave, Pittsburgh PA 15213

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Abstract

Functional lateralization is typically measured by comparing activation levels across the right and left hemispheres of the brain. Significant additional information, however, exists within distributed multi-voxel patterns of activity – a format not detectable by traditional activation-based analysis of functional magnetic resonance imaging (fMRI) data. We introduce and test two methods –one anatomical, one functional– that allow hemispheric information asymmetries to be detected. We first introduce and apply a novel tool that draws on brain 'surface fingerprints' to pair every location in one hemisphere with its hemispheric homologue. We use anatomical data to show that this approach is more accurate than the common distance-from-midline method for comparing bilateral regions. Next, we introduce a complementary analysis method that quantifies multivariate laterality in functional data. This new 'multivariate Laterality Index' (mLI) reflects both quantitative and qualitative information-differences across homologous activity patterns. We apply the technique here to functional data collected as participants viewed faces and non-faces. Using the previously generated surface fingerprints to pair-up homologous searchlights in each hemisphere, we use the novel multivariate laterality technique to identify face-information asymmetries across right and left counterparts of the fusiform gyrus, inferior temporal gyrus, superior parietal lobule, and early visual areas. The typical location of the fusiform face area has a greater information asymmetry for faces than for shapes. More generally, we argue that the field should consider an information-based approach to lateralization.

1. Introduction

The human brain's division into two cortical hemispheres is one of its most visible and clearest organizational principles. Certain cognitive functions are associated with bilateral neural processing, while others are frequently lateralized to one hemisphere (Benson and Zaidel, 1985). For instance, language processing is generally left lateralized (Bradshaw et al., 2017; Friederici and Alter, 2004), and face processing tends to be lateralized in the right hemisphere (Kanwisher et al., 1997). The question of lateralization is important across cognitive domains (Hervé et al., 2013) and remains contentious for some. The reason for lateralized activity during emotion recognition, for instance, continues to be debated, with the 'Right-Hemisphere Hypothesis' (Borod et al., 1998) frequently pitted against the 'Valence-Specific Hypothesis' (Ahern and Schwartz, 1985; Fusar-Poli et al., 2009; though see Killgore and Yurgelun-Todd, 2007). Explanations for the observed right dominance in face recognition are also debated. One explanation is that dominance results from competition with (generally left-lateralized) words, both of which are overlearned and may compete for cortical resources (Behrmann & Plaut, 2013). Alternatively, pre-existing connectivity patterns may play a stronger role in determining eventual lateralization (Saygin et al., 2016). Even the characterization of face perception as right-dominant has recently been questioned (Thome et al., 2022). Lateralization also has clinical relevance, particularly when a clinical group has stronger or weaker lateralization than do healthy controls (e.g., Kylliäinen et al., 2012; Xie et al., 2018). The extent of observed functional lateralization can also predict behavioral responses to presented items (Kaplan and Zaidel, 2001), and track individual differences in how words are processed (Carlos et al., 2019).

Functional lateralization is most often measured by comparing the levels of activation observed in the two hemispheres. For fMRI, this corresponds to tests based on the general linear model (GLM), or ‘activation-based’ analyses, in which task-driven activation in the left and right hemisphere are statistically compared, such as through the Laterality Index (Seghier, 2008). Metrics can rely on thresholding statistical values and comparing the extent of significant activation (Seghier, 2008), or with a threshold-independent measure that allows for more variation in activation levels (Seghier, 2008; Suarez et al., 2009). More recent forms of analysis –specifically, multi-voxel pattern analysis (MVPA)– measure information across patterns of activity distributed across multiple voxels (Haxby et al., 2001). MVPA is particularly useful for investigating how specific perceptual categories (such as faces; Haxby et al., 2001; Kriegeskorte et al., 2007; Axelrod & Yovel, 2012) are encoded in cortex, including at the level of sub-categories or exemplars (Haxby et al., 2001).

Measuring lateralized information

Instead of conceiving of lateralization as a difference in functional activation between corresponding voxels in each hemisphere, we suggest that a difference in *information* is a more comprehensive measure of lateralization. This is an important advance because two regions can exhibit similar activation levels (in traditional univariate analyses), but actually contain different amounts and forms of information (Coutanche, 2013; Haxby et al., 2001). For example, information at different stages of the visual system becomes progressively more independent from early retinotopic organization (Coutanche et al., 2016).

One of the most well-studied lateralized functions (perhaps second only to language) is face processing. Face-selective brain regions have been identified across a large number of studies. Historically, most of these studies identified brain areas that show greater overall activation to faces than to non-faces (Haxby et al., 2000; Kanwisher et al., 1997; Sergent et al., 1992). This is commonly right-dominant (Kanwisher et al., 1997), though activation is also observed in the left fusiform gyrus (e.g., Pourtois et al., 2005; Ramon et al., 2010; Thome et al., 2022). Indeed, some recent evidence from prosopagnosia supports a unique role for left fusiform cortex in the development of the face-processing system (Gerlach et al., 2019).

As noted above, a more recent technique than the univariate approach investigates multi-voxel activity patterns that can encode information that is inaccessible from univariate responses (Haxby et al., 2001). MVPA and related techniques have been used to identify activity patterns that encode faces versus non-faces (Coutanche et al., 2011; Haxby et al., 2001; Spiridon and Kanwisher, 2002), face identity (Anzellotti et al., 2014; Foster et al., 2021; Foster et al., 2022; Guntupalli et al., 2017; Kim et al., 2019; Kriegeskorte et al., 2007; Natu et al., 2010; Nestor et al., 2011; Visconti di Oleggio Castello et al., 2017; though see Weibert et al., 2018 for at-chance between-subject decoding), familiarity (Axelrod & Yovel, 2015; Visconti di Oleggio Castello et al., 2017), symmetry (Flack et al., 2019; Rogers & Andrews, 2022), and social traits and gender (Tsantani et al., 2021). These facial components –identity, familiarity, symmetry, social traits, gender– are capturable by multi-voxel patterns rather than univariate responses partly because they are not fully represented on one dimension (i.e., are multivariate). For instance, it is unlikely that fusiform cortex encodes facial identity based on simple response alone, which would require every face encountered to be recognized via its own unique level (e.g., recognizing Beverly from Deena based on a 2% difference in overall activity). This is all the less likely because other factors like attention modulate fusiform face area (FFA) activity without sudden failures of recognition (Reddy et al., 2007). The ability to pool the unique contributions of voxels also gives greater sensitivity to more nuanced and subtle patterns in brain activity (Coutanche, 2013).

Some MVPA studies of face processing examine right, but not left, fusiform cortex (e.g., Coutanche et al., 2011; Tsantani et al., 2021). Others examine both left and right fusiform together by combining them into one bilateral ROI (Flack et al., 2019; Foster et al., 2021; Foster et al., 2022; Weibert et al., 2018) with no aim of comparing them. A subset of studies investigate the two sides independently, by reporting decoding performance from each set of left and right voxels (Axelrod & Yovel, 2015; Guntupalli et al., 2017; Kim et al., 2019; Nestor et al., 2011; Rogers & Andrews, 2022; Visconti di Oleggio Castello et al., 2017). Notably, these analyses of left and right decoding will statistically test each fusiform homologue but not compare or examine them further.

How might one assess lateralization of information in multi-voxel patterns? Such information can differ quantitatively and qualitatively. For comparing quantity, we can contrast how well activity patterns can be used to discriminate conditions, such as through decoding accuracy (Figure 1, right). For instance, activity patterns in the left visual word form area can discriminate viewed words from letter-strings to a greater degree than can its right homologue (Carlos et al., 2019). A significant difference here indicates an asymmetry in detectable information (assuming equal signal-to-noise; see discussion). This does not mean, however, that similar decoding accuracies reflect identical (‘redundant’) information.

Qualitative differences, on the other hand, occur when two regions encode different types of information, or dimensions, such as facial configuration versus features. Such qualitative differences can be assessed in a number of ways, including comparing which conditions can be classified and classifier performances (Tong & Pratte, 2012; see Discussion for more). It is important to note that both quantitative and qualitative differences can occur together (i.e., they are not mutually exclusive), making their identification complex.

Here, we introduce a method of detecting both quantitative and qualitative differences across hemispheres. We term this, 'multivariate Laterality Index' (mLI). Readers are referred to the Methods for full details, but briefly, the method asks if combining voxels from both hemispheric homologues together has more information than each alone. This is tested by asking if a classifier based on voxels from both homologues can decode conditions with greater accuracy than the homologues separately; Figure 1, right). This is the first time, to our knowledge, that hemispheric homologues have been compared in this way.

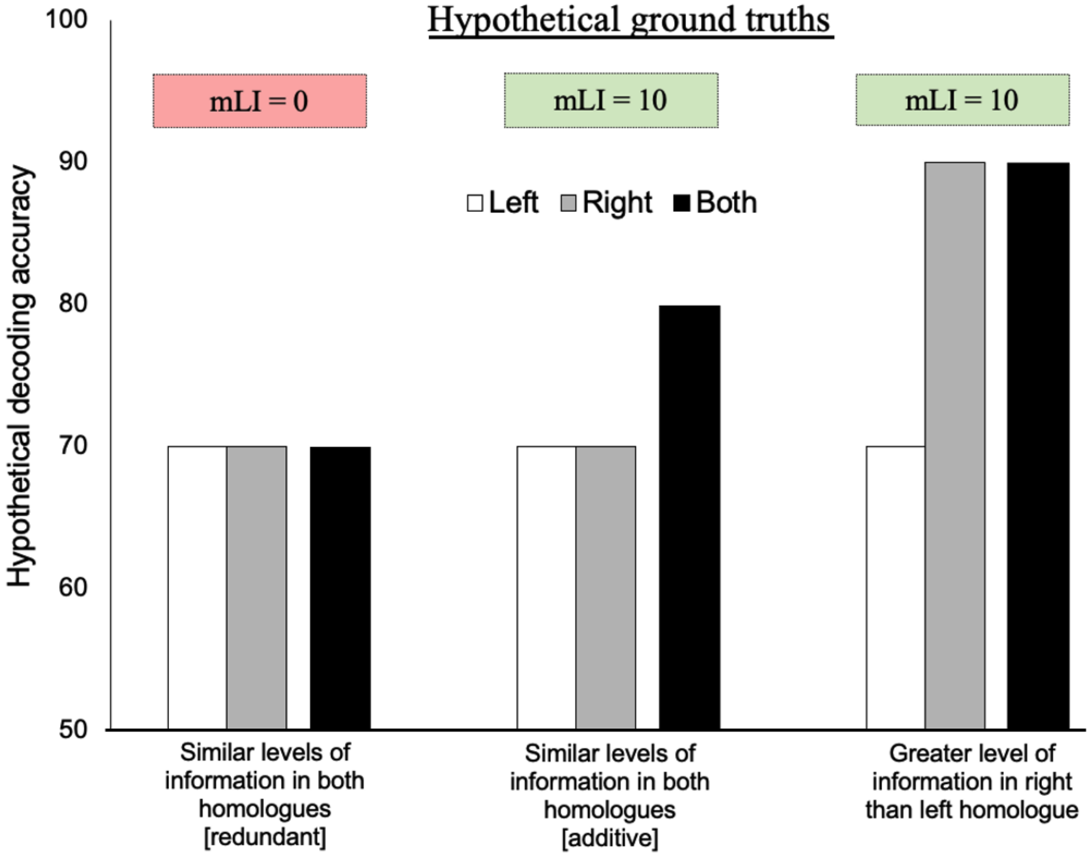

Figure 1: Potential ground truths and associated mLI values. mLI values are calculated by decoding using voxels from both homologues, and subtracting the mean decoding performance from analyzing left and right voxels independently. When information is similar quantitatively and qualitatively (left), mLI is zero. mLI is positive when decoding performance is similar with additive information (center), or when decoding is greater in one hemisphere (right).

Locating homologues for analysis

When examining lateralization for an identified region of interest (ROI), it is naturally necessary to locate the equivalent contralateral site (homologue). One common approach is to use the ROI's distance from the brain's midline, usually using Talairach or MNI coordinates (Johnstone, Karlsson, & Carey, 2020; e.g., Westerhausen, Kompus, & Hugdahl, 2014). In coordinate systems such as Talairach and MNI, X-coordinates originate at the brain's midline, such that negative and positive coordinates reflect left and right regions. If a cognitive function can be localized, an independently localized ROI can be compared to an equivalently sized ROI in the other hemisphere with a similar distance-from-midline (e.g., Davies-Thompson et al., 2016; Nielsen et al., 2013). An important limitation of relying on Euclidean distance in three-dimensional voxel space is that idiosyncrasies (and asymmetries) of gyri and sulci in each hemisphere are not taken into account. This is particularly a risk because of the convoluted shape of neocortex, in which two voxels might be adjacent in voxel-space, but (due to a sulcus between them) might actually be far apart in cortical space (Figure 2). Part of this is solved by switching to surface-based analyses: flattening cortical folds to form a surface (Fischl et al., 1999) allows the true distance between two points to be measured. This 'flat map' of each hemisphere might still be anatomically asymmetrical (due to variations in the shape and size of anatomical structures), but distance along the surface will more accurately reflect cortical distance.

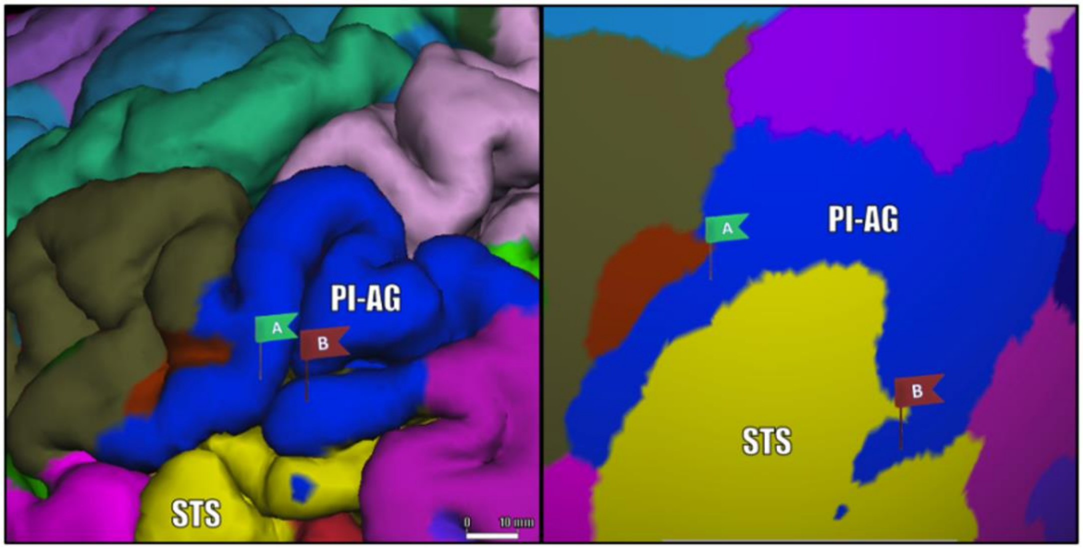

Figure 2: Illustration of Euclidean distance between two points in three-dimensional voxel space versus flat space along the cortical surface. For this given subject's left hemisphere, two markers within the parietal inferior angular gyrus (PI-AG) illustrate their apparent close spatial distance in voxel space (left), but larger separating distance in surface space (right).

It is worth noting that the imprecision of using distance-from-midline in three-dimensional space is often less of a concern for univariate activation-based studies, than those using MVPA. This is because: i) these studies often focus on spatial specificity at the level of clusters; ii) spatial smoothing spreads-out particular values to neighboring voxels; iii) a region's beta values are often averaged together, to give an overall mean value for each homologue. Spatial imprecision, however, becomes problematic for techniques that use fine-grained spatial patterns, like MVPA, where no (or minimal) smoothing is applied to preserve each voxel's value. Spatial precision also matters when single voxels from other nearby regions can conceivably drive classification accuracy.

A more advanced lateralization approach is to spatially warp one hemisphere to its opposite (e.g., Mazoyer et al., 2016). Guided by structural scans for each individual, the shape of the left hemisphere can be warped to match the exact structure of the right, or *vice versa*.

Unfortunately, one disadvantage is that warping one hemisphere to the other minimizes their structural differences, which may actually be of interest.

To address the challenge of identifying homologous regions while accounting for each individual’s unique anatomy, we introduce a method, ‘Surface Fingerprinting’, that identifies left and right homologue regions using an individual’s unique arrangement of anatomical landmarks. In short (full methods below), the location of every vertex in a hemisphere is marked with its unique set of distances to the center of every anatomically parcellated region in its hemisphere, and then matched with its equivalent vertex in the opposing hemisphere. To anticipate the results, this approach more accurately identifies matching (homologous) populations of voxels, giving greater confidence for methods that depend on spatial precision, such as MVPA and Representational Similarity Analysis (RSA; Kriegeskorte et al., 2008). Here, we combine this with mLI to examine the lateralization of face-related multi-voxel information. We hypothesize that central components of the human face processing system (discussed above; Haxby et al., 2000) will be identified by our analysis, including the commonly right-lateralized FFA, superior temporal sulcus (STS; involved in processing dynamic facial features), and anterior occipital cortex containing the occipital face area (Kanwisher et al, 1997; Haxby et al., 2000; Haxby et al., 2002; Solomon-Harris et al., 2013). Additionally, we predict finding multivariate laterality in (retinotopic) early visual cortex because its left and right regions encode complementary (additive) information from right and left visual fields, respectively (Figure 1 center).

To summarize, here we examine the representation of MVP information across hemispheres. We introduce a new anatomical technique that identifies homologous regions of cortex with greater spatial precision, and examine lateralization of multi-voxel pattern information through a new multivariate laterality index.

2. Materials and Methods

2.1 Data Acquisition and Pre-processing

2.1.1 Subjects

Twenty subjects (12 females; mean age = 22.5 years, SD = 3.9) without neurological or psychiatric disorders were recruited from the University of Pittsburgh community. All participants were right-handed (determined with the Edinburgh Handedness Inventory; Oldfield, 1971), native English speakers, without a learning or attention disorder. Including only right-handed subjects limits variance that would otherwise add noise to the investigated signal, particularly as left-handed individuals have more variable patterns of functional lateralization (Badzakova et al., 2010; Carey and Johnstone, 2014; Rasmussen and Milner, 1977). Although all subjects' anatomical data were included in the Surface Fingerprinting analysis, two subjects were excluded from the subsequent functional analysis due to low behavioral accuracy (more than two standard deviations below the mean of the group), leaving 18 (12 females, mean age = 22.7, SD = 4.1). The study was approved by the University of Pittsburgh's Institutional Review Board and was part of an investigation into number processing (Koch et al., 2023).

2.1.2 Image Acquisition

Participants were scanned at the University of Pittsburgh's Neuroscience Imaging Center using a Siemens fMRI 3T head-only Allegra magnet and 32-channel head coil equipped with mirror device to allow for fMRI stimuli presentation. The scanning session first consisted of a T1-weighted anatomical scan (TR = 1540 ms, TE = 3.04 ms, voxel size = 1.00 x 1.00 x 1.00 mm, 192 slices), followed by T2-weighted functional scans which collected blood-oxygenation-level-dependent (BOLD) signals using a one-shot EPI pulse. Slices were collected in inter-leaved, ascending order (from foot to head), with no skips between slices (TR = 2000 msec, echo time = 25 msec, flip angle = 70°, isotropic voxel size = 3.125 × 3.125 × 3.125 mm, 36 slices, in-plane resolution = 64 × 64, field of view = 200 × 200 mm). The functional scans were collected in four functional runs of 80 volumes each.

2.1.3 fMRI Preprocessing

Preprocessing was performed using Analysis of Functional NeuroImages (AFNI) software (Cox, 1996) and consisted of slice-time correction, motion correction, registration, high-pass filtering, and scaling voxel activation values to have a mean of 100 (maximum limit of 200). The unsmoothed functional data was imported into MATLAB using the Princeton MVPA toolbox (Detre, et al., 2006), which allows easy conversion between three-dimensional AFNI files and two-dimensional matrices in the MATLAB workspace. Once imported in this way, the data was analyzed using MATLAB's ‘fitcnb’ classifier function within a searchlight analysis described below. Functional data were z-scored within each run, and time-points were shifted by three TRs to account for hemodynamic delay.

2.1.4 Experimental Task and Conditions

Subjects completed a traditional match vs. non-match judgment task (Emerson & Cantlon, 2015) in the fMRI scanner. The stimuli conditions were words, faces, quantities and numerals, and shapes. The word condition involved looking at a word printed in lower and uppercase on either side of a fixation cross, and indicating if the words were the same or different. Similarly, the faces condition presented two faces in different orientations and subjects determined if they were the same face or not. The quantities and numeral condition asked whether an Arabic numeral represented the same quantity of dots in an array. Finally, in the shapes condition, subjects were randomized to view geometric shapes or shapes of tools, and determined whether the images reflected the same or different items. Trials lasted two seconds, and were separated by a two-second inter-trial interval (fixation cross). All runs contained two blocks of three trials (at least one match and one non-match) for each of the four conditions. The block order was pseudorandomized to present a block of each condition before proceeding. Blocks were separated by eight seconds of fixation.

2.2 Surface Fingerprinting

The Surface Fingerprinting method identifies left and right homologues. The full codebase for this analysis is available at https://github.com/jakesauter/lateralization_project. To summarize the approach, the location of every vertex in a hemisphere is marked based on its unique array of distances to the center of every anatomically parcellated region in the hemisphere in spherical surface space. This new coordinate system is based on *n* regions (used as reference points) and *v* vertices across the hemisphere, where every vertex has a surface-based distance measurement to every reference point (*n*) on the hemisphere. The closest matching sets of (v,n) coordinates in the two hemispheres are identified as left and right homologues, giving a pairing that is based on the individual's unique surface fingerprint in each hemisphere. Individual steps follow:

1) A subject's anatomical scan is automatically anatomically segmented and labeled, such as through FreeSurfer (e.g., 'recon-all' function), giving a surface-based cortical reconstruction (Fischl et al., 2004; Fischl, 2012). Automated segmentation algorithms can provide anatomical labels with equivalent accuracy as anatomical experts (Destrieux et al., 2011).

The resulting data files, including parcellated surface files, serve as input for the new Surface Fingerprinting coordinate system. This process also generates surface-based spherical coordinates for every vertex of each hemisphere.

2) In each hemisphere's sphere surface (Argall et al., 2006), the center of each uniquely labeled region (e.g., right fusiform gyrus) from the FreeSurfer Cortical Parcellation (Destrieux atlas) is calculated by taking the average spherical coordinates of every vertex assigned to each label. Each central point is used as a reference landmark in the remaining steps (Figure 3).
3) For every vertex (*v*) in a hemisphere, the taxicab distance to each reference landmark (*n*) is calculated and assigned to an *n*-dimensional vector (i.e., set of distances to every landmark). Taxicab distances approximate the length of a curve when taking this many steps through surface space (Thompson, 2011).
4) Once coordinates are established for every vertex of each hemisphere, a vertex's homologue is identified as the vertex with the most similar coordinates in the other hemisphere (i.e., similar distances to 75 reference points – giving a matching anatomical fingerprint).

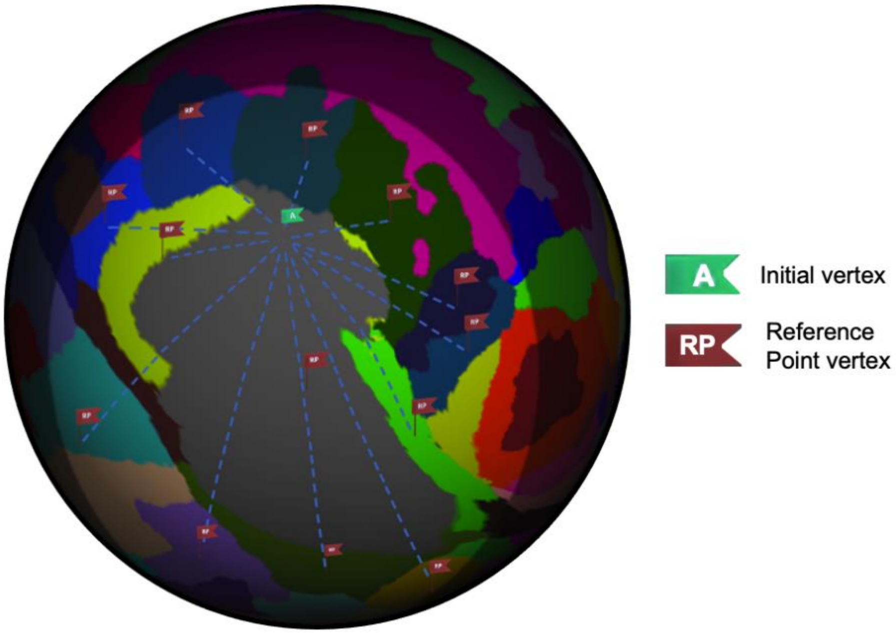

Figure 3: A schematic showing the concept of reference points for a vertex. The distances to every reference point in a hemisphere are measured and compared to distances to the same set of reference points in the other hemisphere. Colors indicate different parcellated regions.

2.3 Application to Anatomical Data

We Surface Fingerprinted T1-weighted anatomical scans from all 20 subjects. To evaluate the method's efficacy, we compared Surface Fingerprinting with the existing distance-from-midline approach (i.e., left and right regions compared based on having identical absolute X-coordinates). To compare methods, we calculated the proportion of paired left and right homologues that successfully fall within the same anatomical label within the hemispheres (e.g., left and right fusiform gyri) for both methods. The ratio of matches to total hemisphere vertices gives an index of success, where higher ratios indicate more vertices being mapped to the equivalently labeled region in the other hemisphere.

2.4 Multivariate Laterality Assessment

To evaluate areas with significant mLI, two whole-brain searchlight analyses were implemented: one discriminating faces from non-faces, and a control searchlight discriminating shapes from non-shapes. To enable their comparison, non-faces did not include shapes, and non-shapes did not include faces. For each searchlight, a Gaussian Naive-Bayes classifier (fitcnb) was trained and tested on patterns of time-shifted TRs through a leave-one-run-out cross-validation framework. The training and testing sets were matched in numbers of trials for each condition by randomly selecting one block from the non-face conditions to match the number of face blocks. The earlier Surface Fingerprinting method matched every vertex with its homologue in the opposing hemisphere (i.e., identifying left and right pairs), where each vertex serves as the center for a searchlight. Each searchlight (mean = 299.3 vertices) included neighboring vertices out to a distance threshold of 5% of the maximum distance to landmarks. This is computationally efficient because such distances are pre-calculated in the prior Surface Fingerprinting.

For each homologous pair of searchlights (i.e., left and right), multivariate laterality was calculated as follows. First, the features of the two searchlights were concatenated and used for classification. The resulting accuracy reflects information from both hemispheres. The mean accuracy of the individual left and right searchlights is then subtracted from the combined accuracy. This value, which we term ‘Multivariate Laterality Index’ (mLI), reflects the presence of information differences across hemispheres – for either quantitative and qualitative differences (Figure 1). Comparing bilateral (i.e., combined) decoding performance to the *mean* performance of the separate ROIs allows us to detect both quantitative and qualitative differences. One alternative would be to compare bilateral performance to the maximum decoding performance of the two regions, but this would not detect purely quantitative differences. For instance, it is reasonable to consider the case of one homologue having more detectable information than the other as reflecting multivariate laterality (even if the information is redundant across homologues), but this would not be detected based on a comparison with the homologues’ maximum decoding performance: this would generate the same value as when two homologues have identical amount of detectable information (i.e., no laterality). On the other hand, contrasting the combined performance with the average of the homologues allows us to distinguish these scenarios (see Figure 1). To dig deeper into the features of the detected multivariate laterality, we follow-up by examining how decoding performance differs across hemispheres within the areas with significant mLI.

The above mLI values from each individual were then submitted to a secondary group analysis. To visualize the results, we mapped these results onto standard left-hemisphere meshes with linear depth density 60 via the AFNI command SurfToSurf. The values on this left-hemisphere mesh reflect the mLI, which is calculated from both hemispheres. The AFNI 3dttest++ command tested 'combined minus average of individual hemispheres' against zero. To correct for multiple comparisons, we first obtained a dataset of noise for each subject by conducting permutation testing with a searchlight analysis using randomized condition labels. These noise maps were standardized and averaged to form a group dataset of noise using the AFNI 3dMean function. This group dataset was given as an argument to the AFNI SurfFWHM function to generate an estimate of smoothing based on data thresholded at an uncorrected alpha of .01. This smoothing estimate was then used to calculate corrected alpha = .01 cluster sizes with AFNI's slow_surf_clustsim.py.

3. Results

3.1 Anatomical Results: Surface Fingerprinting

We first asked if the new Surface Fingerprinting method is significantly more accurate than the existing distance-from-midline approach. Surface Fingerprinting successfully identified left and right homologues that fell within matching atlas labels in a significantly greater (paired t-test: $t(19) = -30.65$, $p < .001$) number of vertices: 79.3% (*SD* = 0.01), compared to 64.2% (*SD* = 0.03) from the distance-from-midline approach (Figures 4 and 5). The superiority of Surface Fingerprinting was consistent across all subjects, as reflected in their respective ranges: 77.47 - 80.68% (Surface Fingerprinting) versus 58.84 - 70.60% (distance-from-midline).

Distance-from-midline

Surface Fingerprints

Figure 4: An example subject, showing correct label matches for left and right homologues, identified through distance-from-midline (top) and Surface Fingerprinting (bottom) methods. Green indicates correct labeling; gray indicates a mismatch. This subject has distance-from-midline matches of 64.74%, and Surface Fingerprints matches of 80.13%. Left hemisphere depictions are shown of posterior (left), lateral (middle), and inferior (right) views.

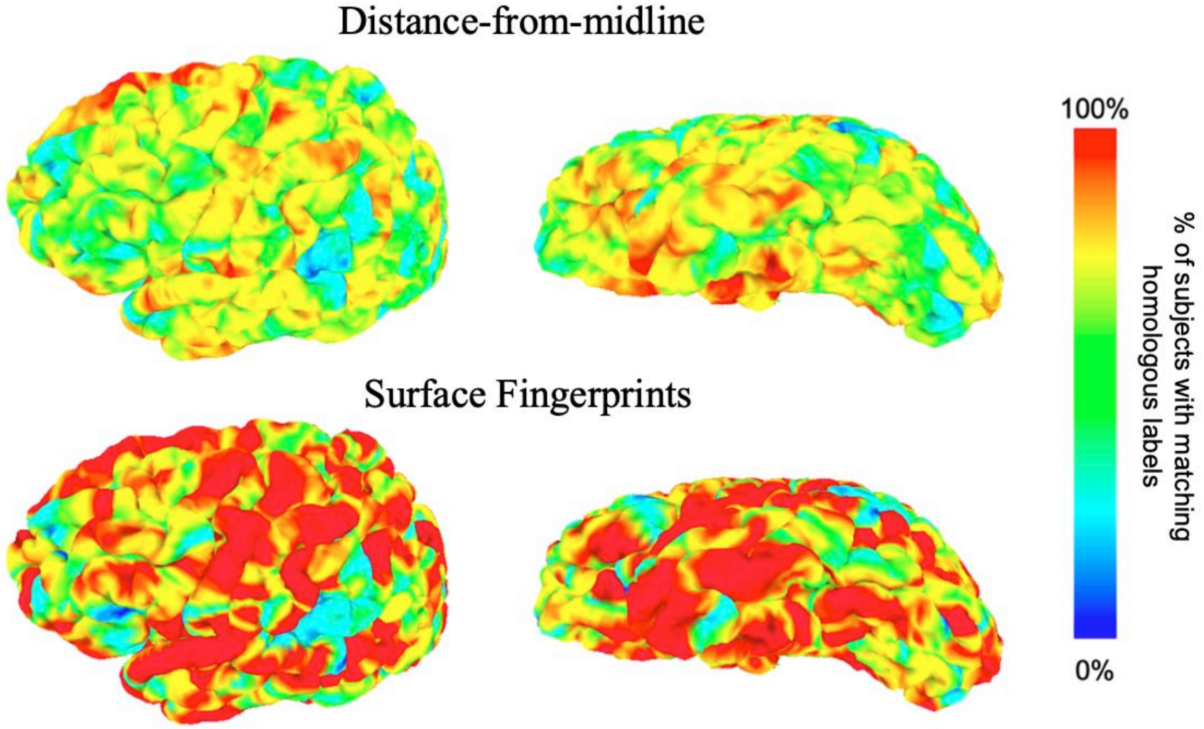

Figure 5: A group map of homologue label matches for each method. The color gradient reflects the percentage of subjects with homologous matches with atlas labels. Left hemisphere depictions of lateral and inferior views.

3.2 Searchlight Results

Face searchlight

We next examined the asymmetry of information across hemispheres. After cluster-correction for multiple comparisons (637 mm^2 minimum, corrected p = .01), we identified multivariate laterality (via significant mLI) in two large clusters: the first encompassing the fusiform gyrus, inferior temporal gyrus, inferior occipital gyrus, and occipital pole (Talairach X = -31, Y = -76, Z = -17; Figure 6), and a second in the superior parietal lobule (Talairach X = -16, Y = -78, Z = 41).

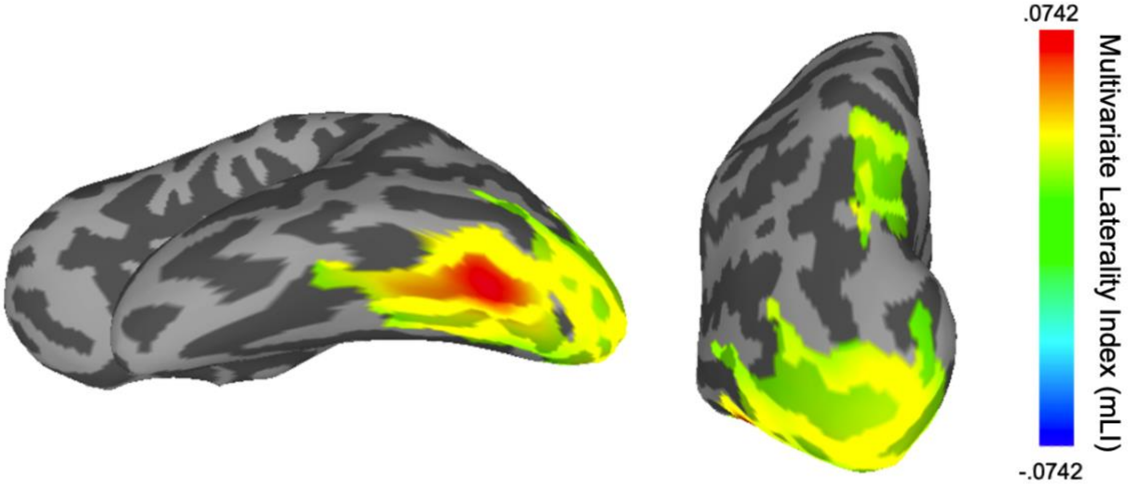

Figure 6. Multivariate laterality from classification of faces versus non-faces, displayed on inflated left hemisphere surface mesh. Clusters have a minimum surface area of 637 mm^2 (giving corrected p = .01)

Shape searchlight

Multivariate laterality was also analyzed for shapes. One cluster survived the cluster corrections procedure, encompassing the fusiform gyrus, inferior occipital gyrus and sulcus, and occipital pole (peak at Talairach X = -34, Y = -68, Z = -11; Figure 7).

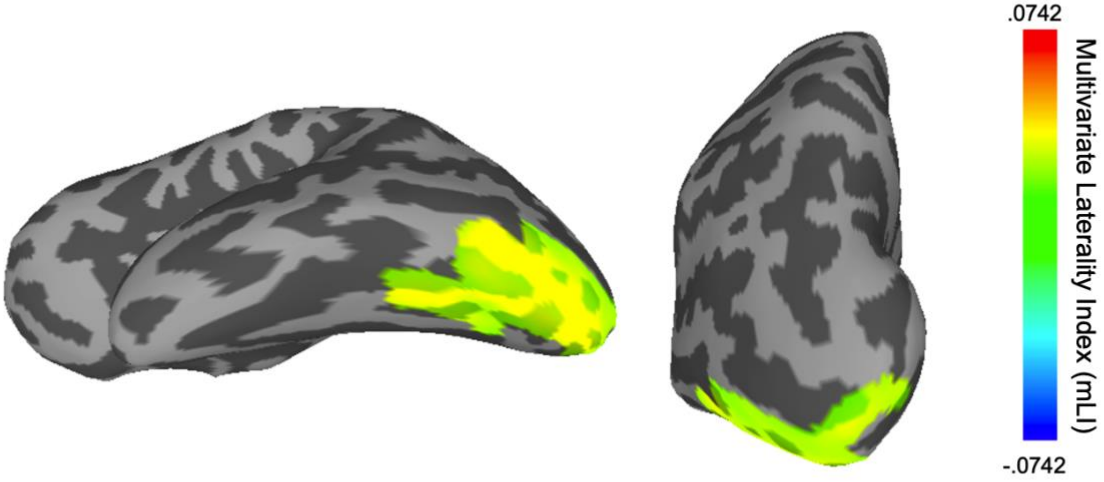

Figure 7. Multivariate laterality from classification of shapes versus non-shapes, displayed on inflated left hemisphere surface mesh. Clusters have a minimum surface area of 637 mm^2 (giving corrected p = .01)

Comparing face and shape mLI

We next statistically compared the face and shape mLI values in a within-subjects analysis using the ‘paired’ option within 3dttest. One cluster survived correction, in the fusiform gyrus and lateral occipitotemporal sulcus (peak at X = -34, Y = -68, Z = -11; Figure 8). All vertices in this cluster had greater mLI values for faces compared to shapes.

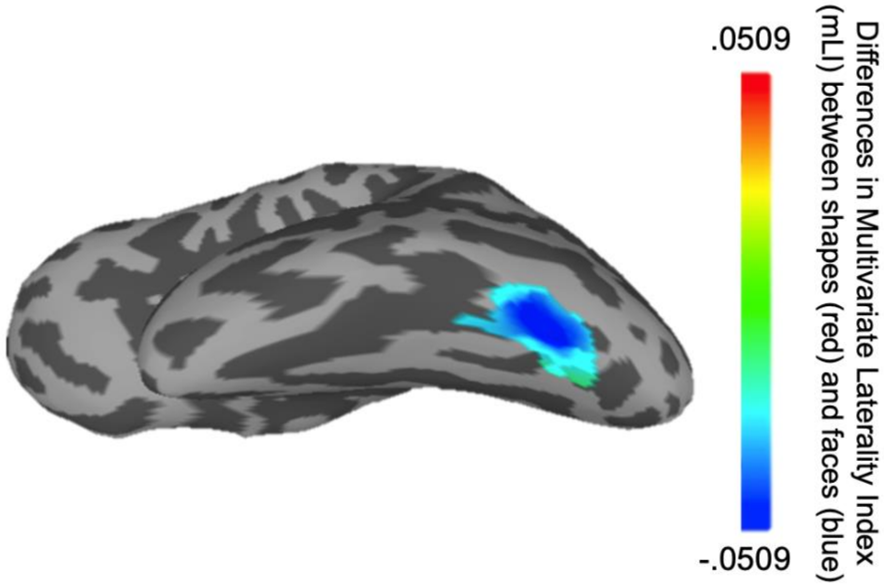

Figure 8. Difference in multivariate laterality between shapes (red) and faces (blue) displayed on inflated left hemisphere surface mesh. Clusters have a minimum surface area of 637 mm^2 (giving corrected p = .01)

The cluster identified above shows a significantly greater mLI for faces than for shapes. The identified region is in the typical area of the FFA. To verify this –while avoiding potential concerns about double-dipping through using the same data– we drew on Neurosynth, an automated meta-analytic tool that reports the terms associated with particular brain locations from the neuroimaging literature (Yarkoni et al., 2011). The location identified in the above face versus shape comparison was analyzed across the 299 studies reporting activation within 6 mm of these coordinates. In the right hemisphere, face-related terms were the main function reported (after anatomical labels): in descending order of association strength: right side: *fusiform* (*z* = 8.07), *faces* (*z* = 6.66), *fusiform gyrus* (*z* = 6.58), *occipital* (*z* = 5.99), *visual* (*z* = 5.78), *fusiform* *face* ($z = 5.77$); left side: *fusiform* ($z = 10.22$), *visual* ($z = 7.84$), *fusiform gyrus* ($z = 7.44$), *occipital* ($z = 6.58$), *occipitotemporal cortex* ($z = 6.48$), *occipitotemporal* ($z = 6.42$). Calculating significance *p*-values from these results is complex and discouraged (Yarkoni et al., 2011) but the dominance of face-related terms from the meta-analysis is consistent with this location (of greater mLI for faces) falling within the FFA.

To characterize the information-differences across hemispheres, we computed and displayed right minus left decoding accuracies for the areas that were identified by the multivariate laterality analysis (Figure 9). Higher absolute values indicate hemispheric differences in decoding performance (i.e., quantitative differences). Values near zero reflect the presence of similar decoding performance across homologues (e.g., 70% in each), with greater performance when combined (e.g., 80%; leading to the significant mLI). This latter case reflects additive information in the two hemispheres (qualitative differences). For instance, here, this is apparent in posterior occipital cortex (early visual cortex; EVC) as one would expect – the left and right areas of EVC are each responsible for responses to one half of the visual field (right and left, respectively). Each visual field might give similar classification performance from their respective activity patterns, but will give greater decoding performance when combined (because this reflects neural responses to the whole image, rather than just the left or right half of the visual field). On the other hand, areas showing greater values have differences in overall decoding performance (i.e., one homologue has a greater ability to decode the stimulus categories, than does the other).

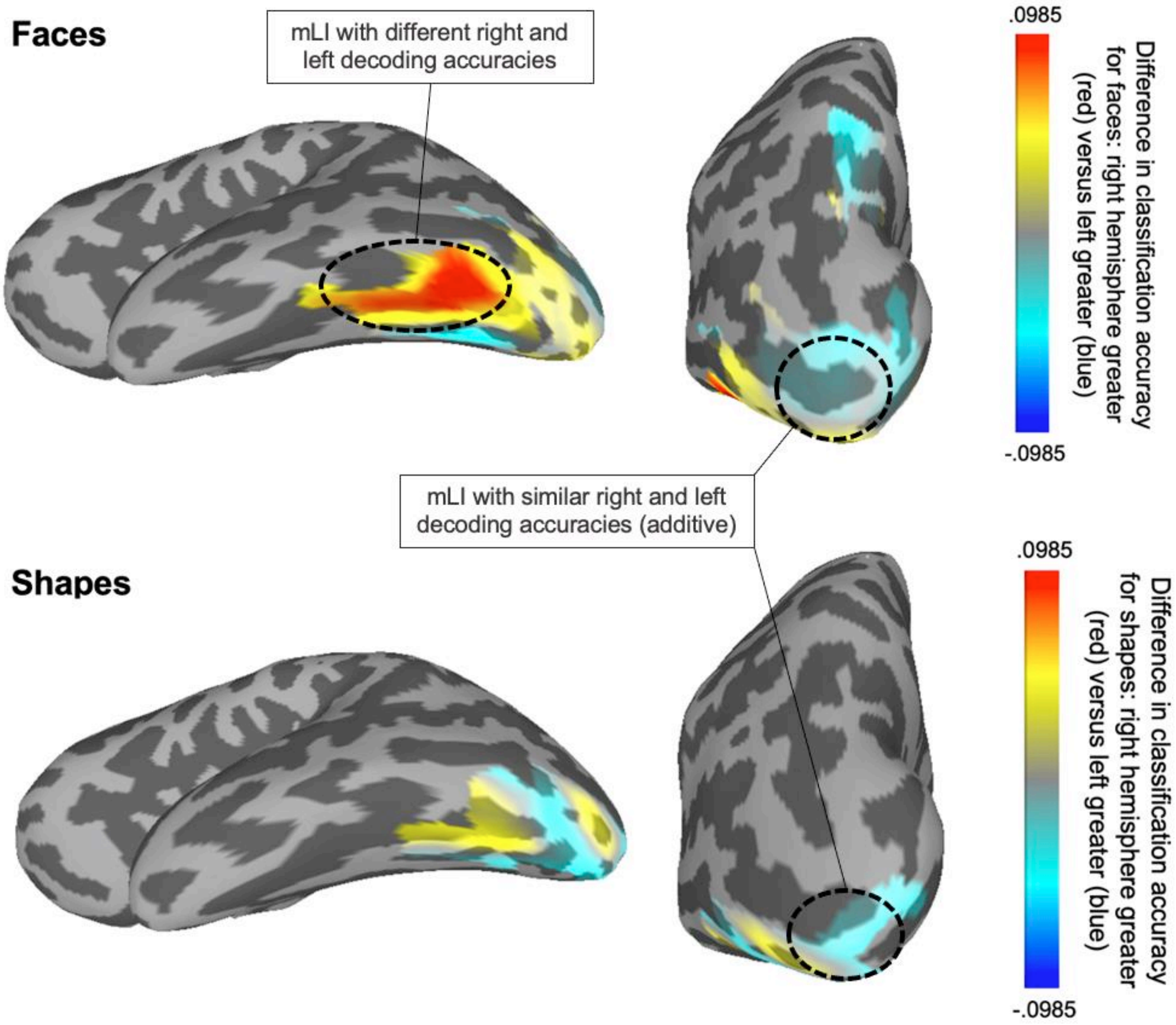

Figure 9. Differences in classification performance between the right and left homologues within the significant mLI clusters previously identified. Faces (top) and shapes (bottom) are illustrated on an inflated left hemisphere surface mesh. Because all areas were significant in the prior multivariate laterality analysis, vertices with values near zero have similar classification performance across hemispheres (e.g., 70% in each) but greater performance when combined (e.g., 80%).

4. Discussion

We have introduced and tested two methods that advance the examination of lateralization. The first, Surface Fingerprinting, identifies homologous areas in the left and right hemispheres with greater accuracy than an existing method. Using multiple vectors to identify corresponding areas in the left and right hemispheres proved to be more accurate than a typical distance-from-midline approach. This is particularly valuable for methods sensitive to the contribution of individual voxels, such as MVPA. Second, we introduce a way to measure hemispheric differences in multi-voxel information (computed as mLI). We apply the approach to functional data collected as participants viewed faces, shapes and other categories of images. We detected greater multivariate laterality for faces than shapes in an area consistent with the location of the FFA, giving validity to the method, and advancing the characterization of how fusiform cortex encodes faces.

Our hypothesis that EVC would have additive information was borne out: decoding with both hemispheres of this area was greater than the average of each hemisphere alone (significant mLI) despite the left and right homologues having similar (independent) decoding performance. This means that the significant mLI is due to the two hemispheres holding additive information, likely due to their respective roles in processing stimuli in the right and left visual fields (as well as other information; Coutanche & Koch, 2018).

In considering this method and results, we may ask what we really mean by "lateralization". A classic interpretation is a cognitive function being associated with greater use of one hemisphere than the other. Magnitude of activation is typically used as a proxy for 'use', but we argue that it is beneficial to reframe the issue as a question of the presence of *information*. A large number of studies have identified situations in which multi-voxel patterns reflect information that is not apparent from univariate activation (Harrison & Tong, 2009; Haxby et al., 2001). In the context of existing laterality measures, which can be threshold-dependent (binarized) or threshold-independent (continuous; Seghier, 2008; Suarez et al., 2009), mLI is closer to threshold-independent because each participant's multivariate laterality is quantified continuously – any sub-threshold information contributes to the subsequent group analysis.

Once multivariate laterality is identified in a study, researchers will likely wish to investigate its particular nature. As discussed above, hemispheric differences can be quantitative (e.g., different decoding accuracies) or qualitative (with different bases for separating conditions; Figure 1). The first can be measured by directly comparing decoding performance for key conditions, as has been performed for different stages of the visual system (Coutanche et al., 2016). The second is more difficult but can be achieved in several ways. One way is to ask if the information across hemispheres is additive or redundant. Additive information is reflected by an increase in decoding performance when drawing on both homologues, compared to each individually. Another is to compare the dimensions (principles) on which conditions are separable in regions' neural activity, through examining classifier confusion matrices or representational dissimilarity matrices. The mLI metric we introduce is able to detect either quantitative or qualitative differences through one measure.

When applied to this dataset, we identified multivariate laterality in core areas of the face network: the fusiform gyrus, STS, inferior occipital cortex (Kanwisher et al, 1997; Haxby et al., 2000; Haxby et al., 2002; Solomon-Harris et al., 2013). This follows prior work showing that FFA activity is consistently greater in the right hemisphere (Kanwisher et al., 1997), but that bilateral activation is also often observed (Thome et al., 2022), indicating a role for the left face processing network. Behavioral data from split-brain patients also support hemispheric asymmetry for identifying gender (Prete et al., 2016) and age (Prete and Tommasi, 2018) from faces. If we consider the left and right hemispheres as sources of distinct but complementary information about general and individual faces, it becomes more appropriate to conceptualize face perception in a complex bilateral network of information, rather than a purely 'right hemisphere' function.

The utility of these new methods are not confined to faces; word processing, for example, is another lateralized function that may draw on fusiform cortex homologues (Carlos et al., 2019). Surface Fingerprinting is also suited for clinically relevant hemispheric differences (Coutanche and Hallion, 2020; Coutanche et al., 2011) because Surface Fingerprints maintain individuals' cortical map idiosyncrasies, so that important clinical differences are not 'standardized-out'. Similarly, quantifying hemispheric growth or atrophy, examining developmental trajectories, and tracking aging, could benefit from Surface Fingerprinting.

The techniques we introduce and demonstrate are subject to certain limitations and caveats. First, it is always possible that increases in decoding performance can be driven by a reduction in noise from adding a less noisy voxel to the analyzed (bilateral) region. This is relevant to any decoding study that compares decoding performance across ROIs (Kriegeskorte & Douglas, 2019). That said, we believe this risk is not high here because any significant effects would need to occur across multiple participants in the same location due to the group analysis. Relatedly, the signal-to-noise drop-outs experienced in BOLD activity are usually bilateral, rather than increasing noise selectively in one hemisphere. Another reason to be confident is our EVC results, which show similar levels of decoding performance across hemispheres *with* significant mLI. This fits with our hypothesis that the additive organization of right and left EVC serving left and right visual fields would be detected. This does not rule-out a role for noise in other regions, but shows that it is possible to have multivariate laterality with similar decoding accuracies.

An additional caveat is that although we have applied the technique through a searchlight exploratory approach, certain uses may benefit more from the use of a localizer. Surface Fingerprinting can identify the homologous region to a unilateral area, but in cases where bilateral regions are apparent from activation, an independent localizer may be preferential. That said, it is worth noting that for MVPA, an optimal area based on univariate activation might not match an optimal location identified through multivariate information. It is possible to localize functionality based on decoding performance across searchlights (e.g., see Carlos et al., 2019). To avoid interpretive difficulties, researchers might wish to use a matching localizer and laterality metric (i.e., multivariate searchlight localizer for multivariate laterality; univariate localizer for traditional univariate laterality). Future studies might also investigate functions that are currently considered bilateral, to ask if the quantity or character of multivariate information is actually lateralized.

In summary, Surface Fingerprinting allows regions in one hemisphere to be compared to their closest equivalent in the opposite hemisphere. Surface Fingerprinting identified anatomically-matching hemispheric homologues significantly more accurately than existing distance-from-midline approaches. This method is particularly useful for examining multi-voxel patterns, which rely on spatially accurate comparisons. We have introduced a new functional metric of multivariate laterality (mLI), and show that it can identify information asymmetries during face and shape processing. Overall, we hope this encourages further work in questions of information-representation across hemispheres.

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