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Differential functional reorganization of ventral and dorsal visual pathways following childhood hemispherectomy

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ABSTRACT

Hemispherectomy is a surgical procedure in which an entire hemisphere of a patient's brain is resected or functionally disconnected to manage seizures in individuals with drug-resistant epilepsy. Despite the extensive loss of both ventral and dorsal visual pathways in one hemisphere, pediatric patients who have undergone hemispherectomy show a remarkably high degree of perceptual function across many domains. In the current study, we sought to understand the extent to which functions of the ventral and dorsal visual pathways reorganize to the contralateral hemisphere following childhood hemispherectomy. To this end, we collected fMRI data from an equal number of left and right hemispherectomy patients who completed tasks that typically elicit lateralized responses from the ventral or the dorsal pathway, namely, word (left ventral), face (right ventral), tool (left dorsal), and global form (right dorsal) perception. Overall, there was greater evidence of functional reorganization in the ventral pathway than in the dorsal pathway. Importantly, because ventral and dorsal reorganization was tested within the very same patients, these results cannot be explained by idiosyncratic factors such as disease etiology, age at the time of surgery, or age at testing. These findings suggest that because the dorsal pathway may mature earlier, it may have a shorter developmental window of plasticity than the ventral pathway and, hence, be less malleable after perturbation.

1. Introduction

In adulthood, damage to higher-level regions of visual cortex, for example, following traumatic insult, stroke, or surgery, causes profound visual processing deficits. The anatomical origins of many of these deficits are lateralized, such that damage to the left versus right hemisphere may cause a distinct pattern of impairment. For instance, in the ventral visual pathway, damage to portions of the left hemisphere of the ventral occipital temporal cortex (VOTC) commonly results in deficits in perceiving and recognizing written text (Behrmann et al., 1990, 1998; Cohen et al., 2003), whereas damage to portions of the right hemisphere VOTC commonly leads to deficits in face recognition (Albonico and Barton, 2019; Landis et al., 1986; Rossion, 2022). Similarly, in addition to impairing types of actions like reaching and grasping (Goodale et al., 1994; Goodale and Milner, 1992), lateralized damage to the dorsal pathway can cause perceptual deficits. For instance, damage to the posterior parietal cortex (PPC) of the left hemisphere may cause deficits in understanding how to use objects as tools (Garcea et al., 2018; Johnson-Frey, 2004), whereas damage to portions of the right hemisphere may cause deficits in perceiving global object form (Karakose-Akbiyik et al., 2023; Romei et al., 2011). In adults, these deficits may be longlasting and, even with intervention, may never recover fully (Behrmann et al., 2005; Behrmann and McLeod, 1995).

In contrast to adults, however, accumulating evidence suggests that similar (or even greater) disruptions to cortex in childhood may not result in deficits as severe as those observed in adulthood (Bourne, 2010; Kolb and Gibb, 2011). Indeed, children who undergo large-scale surgical resections of VOTC show strong recognition abilities and demonstrate

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neural reorganization of word and face representations to spared regions of cortex. For instance, pediatric patients who had portions of their left VOTC removed, encompassing regions crucial for reading (i.e., visual word form area; VWFA), nevertheless learn to read and evince selectivity to written words in their preserved right hemisphere (Liu et al., 2019, 2018). Similarly, patients who had portions of their right VOTC removed, encompassing regions crucial for face perception (i.e., fusiform face area; FFA), nevertheless recognize faces and demonstrate face selectivity in their preserved left hemisphere (Liu and Behrmann, 2017). Indeed, pediatric patients with left or right ventral resections show surprisingly high accuracy on face and word recognition tasks that is only modestly, albeit statistically, lower than controls (Granovetter et al., 2022). Thus, unlike in adulthood, the developing ventral pathway may be sufficiently plastic to permit reorganization following large-scale damage.

Much less is known about the degree to which the dorsal visual pathway reorganizes following damage in childhood. Some researchers have hypothesized that the dorsal pathway may be particularly vulnerable to disruption in childhood relative to the ventral pathway – resulting in permanent and long-lasting deficits (Braddick et al., 2003; Grinter et al., 2010). Indeed, the developmental disorders that most commonly cause visual impairments in children are those that affect dorsal processing (Flanagan et al., 2003). These include cerebral visual impairment (CVI), Fragile X syndrome, William's syndrome, and cerebral palsy (Grinter et al., 2010; Macintyre-Béon et al., 2010). These children demonstrate poor performance on tasks dependent on the dorsal pathway, such as global motion perception (Jakobson et al., 2006), motor coordination (Hocking et al., 2008), and visuospatial processing (Bellugi et al., 2000; Cornish et al., 1998, 1999), while demonstrating spared performance on tasks linked to the ventral pathway, such as visual object recognition.

One possible explanation for the greater vulnerability of the dorsal pathway is that it matures earlier than the ventral pathway and, therefore, has a smaller window of plasticity – making it less resilient to disruption. Indeed, studies with typically developing human and non-human primates have shown that the anatomical cytoarchitecture of PPC is more adult-like than the VOTC in infancy and early childhood (Ayzenberg and Behrmann, 2022a; Bourne and Rosa, 2006; Ciesielski et al., 2019; Distler et al., 1996). Furthermore, human and monkey neonates exhibit more mature magnocellular than parvocellular processing (Hammarrenger et al., 2003; Kogan et al., 2000; Rakic et al., 1977), which are the primary subcortical inputs to dorsal and ventral pathways, respectively. Thus, because the structure of the dorsal pathway is in place, or stable, earlier in development than the ventral pathway, it may be less amenable to reorganization following disruption. However, comparisons between ventral and dorsal pathways are difficult to measure in most pediatric patient populations because there are many patient-specific factors that influence how well a patient recovers, such as the extent of damage, etiology of the disease, age of onset of damage, as well as age at the time of surgery.

One recent study sought to overcome some of these limitations by testing a patient with damage to both dorsal and ventral pathways. Specifically, Ahmad et al. (2022) conducted a study with patient TC who had areas of both her left PPC and VOTC surgically removed to treat drug-resistant epilepsy. They found that TC was impaired on tasks that required dorsal pathway processing, namely, grasping a block with her fingers, but not on tasks that required ventral pathway processing, namely, pantomiming or visually matching the size of a block using her fingers. Thus, although TC's left dorsal and ventral pathways were removed concurrently, these findings suggest that functions supported by the ventral pathway recovered, whereas those supported by the dorsal pathway did not. Importantly, because they tested dorsal and ventral capacities in a single patient with damage to both pathways, they were able to rule out alternative explanations related to age at time of surgery and other aspects of disease etiology.

Although TC's pattern of deficit suggests that ventral and dorsal pathways showed differential capacity for reorganization, there remain several open questions. For instance, it is unclear whether the two pathways were equally damaged, and, thus, whether TC's intact visual matching abilities reflects greater sparing of VOTC tissue relative to PPC. Furthermore, it is unclear to what degree each task involved lateralized processing or could be accomplished with either hemisphere. For instance, the grasping task may have required relatively more input from the left hemisphere compared to the visual matching task. Indeed, it is unclear to what degree visual matching is lateralized to one hemisphere. In other words, visual matching might not rely on left VOTC as much as grasping relies on left PPC. Thus, one explanation for TC's performance on the visual matching task is not that the capacities of the ventral pathway recovered, but that her visual matching abilities were only minimally disrupted in the first place. By contrast, because motor movements, such as grasping, are primarily supported by the contralateral hemisphere, a greater degree of reorganization would be needed to recover normal grasping abilities.

In the current study, we sought to overcome these methodological challenges by testing patients with resections, or disconnections, of both ventral and dorsal pathways, and by using tasks that are known to elicit lateralized processing in each pathway. Specifically, we conducted functional magnetic resonance imaging (fMRI) with patients who had undergone childhood hemispherectomy surgery – a removal or disconnection of an entire hemisphere – while they completed functional localizer tasks designed to elicit lateralized responses from left or right ventral or dorsal pathways. These included localizers for word and face processing regions, which are known to elicit greater responses in left and right VOTC, respectively (Behrmann and Plaut, 2020), as well as localizers for tool and object global form regions, which are known to elicit greater responses in the left and right PPC, respectively (Ayzenberg and Behrmann, 2022b; Garcea and Mahon, 2014).

Hemispherectomy, rather than lobectomy or laser ablation, is undertaken in individuals whose epilepsy typically has multiple foci and leaves little to no cortical tissue in the resected hemisphere (see Fig. 1). In some cases, portions of the frontal and occipital cortex are left intact, but functionally disconnected from the brain stem and other hemisphere, in order to stabilize the remaining hemisphere (Piña-Garza and James, 2019). Remarkably, despite the size of the lesion, these patients generally have good post-surgical cognitive (Devlin et al., 2003; Pulsifer et al., 2004) and visual (Koenraads et al., 2014) outcomes, and, in many cases, show cognitive improvements, especially if the surgery is undertaken early in childhood (Helmstaedter et al., 2020). Importantly, these patients can learn to read (Danelli et al., 2013) and there are few clinical reports of prosopagnosia or object agnosia post-surgery. These findings suggest that the functions of the ventral pathway may have reorganized to the intact contralateral hemisphere.

However, few studies have directly examined the degree to which both ventral and dorsal visual pathways reorganize in the same individual, particularly following an extensive resection as in hemispherectomy. Here, we test a patient population with widespread damage to and resection of ventral and dorsal pathways and use tasks that are known to elicit lateralized processing in healthy participants. In so doing, we can directly test the capacity of the visual system to reorganize and, thereby, can shed light on the developmental trajectory of each pathway. To foreshadow our results, overall, we found that a greater number of hemispherectomy patients showed reorganization in the ventral pathway than the dorsal pathway, potentially supporting the hypothesis that the dorsal pathway matures earlier than the ventral pathway.

2. Materials and methods

2.1. Participants

Eight patients who had undergone hemispherectomy in childhood were recruited (M_{age} = 19.38, Range: 12–37 years) either from the

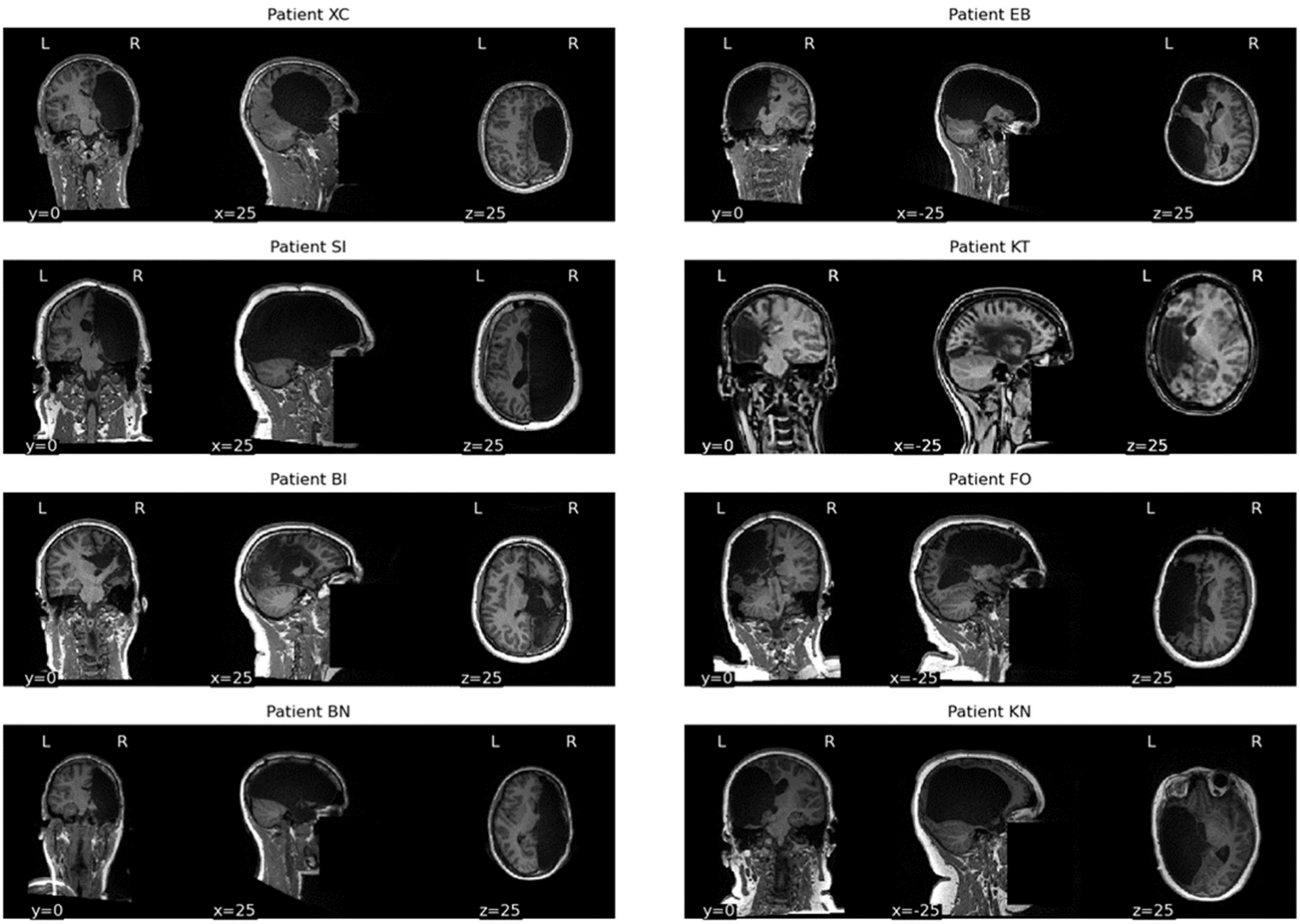

Fig. 1. Anatomical MRI images illustrating the intact and resected portions of each patient's brain. Images have been defaced to protect the identity of each patient.

Pediatric Epilepsy Surgery Program at University of Pittsburgh Medical Center Children's Hospital of Pittsburgh or the Pediatric Epilepsy Surgical Alliance. Of these, four patients had right hemispherectomies (patients: XC, SI, BI, BN) and four had left hemispherectomies (patients: EB, KT, FO, KN). Each patient completed four localizer tasks designed to elicit a lateralized response in the left or right ventral and dorsal pathways: words (left ventral), faces (right ventral), tools (left dorsal), and global form (right dorsal), with the exception of patient KT who did not complete the tool localizer due to time constraints during the scanning session. All patients had normal or corrected-to-normal vision in their intact hemifield. For specific patient ages and surgery information, see Table 1.

We also tested 44 control participants ($M_{age} = 22.53$, Range: 13–38 years). Fifteen control participants completed the word and face localizer task, and 18 completed the tool and global form localizer task. These control participants were recruited as part of other ongoing projects (Ayzenberg and Behrmann, 2022b; Liu et al., 2019; Maallo et al., 2020). Six additional participants completed all four tasks. All control participants were right-handed and had normal or corrected-to-normal visual acuity.

All participants and/or their guardians gave informed consent and assent according to a protocol approved by the Institutional Review Board (IRB) of Carnegie Mellon University and the University of Pittsburgh, and received payment for their participation.

2.1.1. *Brief case description*

All patients recruited for this study were seizure-free at the time of testing and were capable of both reading and writing. Patients did not have a clinical history of alexia, prosopagnosia, object agnosia, nor other perceptual disorders such as spatial neglect. Behavioral pre-testing further revealed that patients showed good performance on word, face, and shape recognition tasks, with many patients (though not all)

Table 1
Patient demographic and surgery information. Because several patients underwent revision surgeries, the 'age at surgery' column depicts their age at their most recent surgery. Ages are presented in years. Note, patients who had their surgery before 2-year-of-age reported their surgery age in months, and so these age values are displayed with greater numerical precision.

Patient	Sex	Age at testing	Age at surgery	Surgery Type	Intact Hemisphere
XC	M	17	1.0	Right anatomical hemispherectomy	Left
SI	M	37	11.0	Right anatomical hemispherectomy	Left
BI	F	16	1.3	Right hemispherotomy	Left
BN	F	18	9.0	Right anatomical hemispherectomy	Left
EB	F	16	1.1	Left anatomical hemispherectomy	Right
KT	F	15	13.0	Left functional hemispherectomy	Right
FO	F	19	4.0	Left anatomical hemispherectomy	Right
KN	M	12	1.7	Left anatomical hemispherectomy	Right

performing in the range of the controls (see Supplemental Figs. 1 and 2 for results for each patient). Patients are hemianopic with blindness of the visual field contralateral to their resected hemisphere, but have normal, or corrected-to-normal vision, in the intact visual field. Patients accurately fixate by moving their head or eyes towards a target stimulus (Chroneos et al., 2023). Patients are hemiplegic with impaired motor control of limbs contralateral to the *resected* hemisphere. motor control of limbs contralateral to their *intact* hemisphere is unimpaired. Indeed, patients successfully use their hand for fine motor skills like writing or manipulating cutlery to eat. Thus, under gross observation, patients' behavioral profiles show minimal, if any, evidence of word, face, tool use, or shape perception deficits. For a more detailed exploration of the visual abilities in hemispherectomy patients, see Koenraads et al. (2014).

2.2. MRI scan parameters and analysis

Scanning was done on a 3 T Siemens Prisma scanner at the CMU-Pitt Brain Imaging Data Generation & Education (BRIDGE) Center (RRID: SCR_023356. Whole-brain functional images were acquired using a 64-channel head matrix coil and a gradient echo single-shot echoplanar imaging sequence. Whole-brain, high-resolution T1-weighted anatomical images (repetition time = 2300 ms; echo time = 2.03 ms; voxel size = 1 × 1 ×1 mm) were also acquired for each participant for the registration of the functional images into a common space. The acquisition protocol for each functional run of the word and face localizer consisted of 69 slices, repetition time = 2 s; echo time = 30 ms; flip angle = 79°; voxel size = 3 × 3 × 3 mm, multi-band acceleration factor = 3. The acquisition protocol for each functional run of the tool and global form localizer consisted of 48 slices, repetition time = 1 s; echo time = 30 ms; flip angle = 64°; voxel size = 3 × 3 × 3 mm, multi-band acceleration factor = 4.

All images were skull-stripped (Smith, 2002) and registered to participants' native anatomical space. Prior to statistical analyses, images were motion corrected, de-trended, and intensity normalized. An additional 18 motion regressors generated by FSL were also included. All data were fit with a general linear model consisting of covariates that were convolved with a double-gamma function to approximate the hemodynamic response function. Analyses were conducted using FSL (Smith et al., 2004), and the nilearn and nibabel packages for Python (Abraham et al., 2014).

2.3. Localizer tasks

We administered four localizer tasks designed to elicit a lateralized response in the left or right ventral and dorsal pathways: words (left ventral), faces (right ventral), tools (left dorsal), and global form (right dorsal). Whenever possible, we collected three runs of each localizer task. However, due to participant tolerance and time constraints, some patient and control participants were only able to complete two runs of some tasks. Thus, because each participant contributed at least two runs of a given localizer, we restricted all of our analysis to just two runs of data.

2.3.1. Word and face localizer

On each run of the word and face localizer (378 s), participants viewed blocks of images of words, faces, objects, houses, or box-scrambled images (Figs. 2A and 2B). Each block contained 16 images displaying 15 unique instances, with 1 repeat stimulus randomly inserted per sequence. All stimuli subtended ~4° visual angle on screen. Each image was presented for 800 ms with a 200 ms interstimulus interval (ISI) for a total of 16 s per block. The image order within the block was randomized. Participants viewed 3 repetitions of each block per run in a pre-determined random sequence used for all participants. To maintain attention, participants performed a one-back task, responding to the repetition of an image on consecutive presentations. Word representations were measured as a greater response to the word condition than the object condition. Similarly, face representations were measured as a greater response to the face condition than the object condition.

2.3.2. Tool localizer

On each run of the tool localizer (340 s), participants viewed blocks of object images that contained tools (tool condition), manipulable non-tool objects (non-tool condition), or box-scrambled object images (scrambled conditions; Fig. 2C). Following previous work (Mahon et al., 2007), we defined tools here as manipulable objects whose physical form is directly related to their function (e.g., a hammer). By contrast, manipulable non-tool objects are those that can be arbitrarily

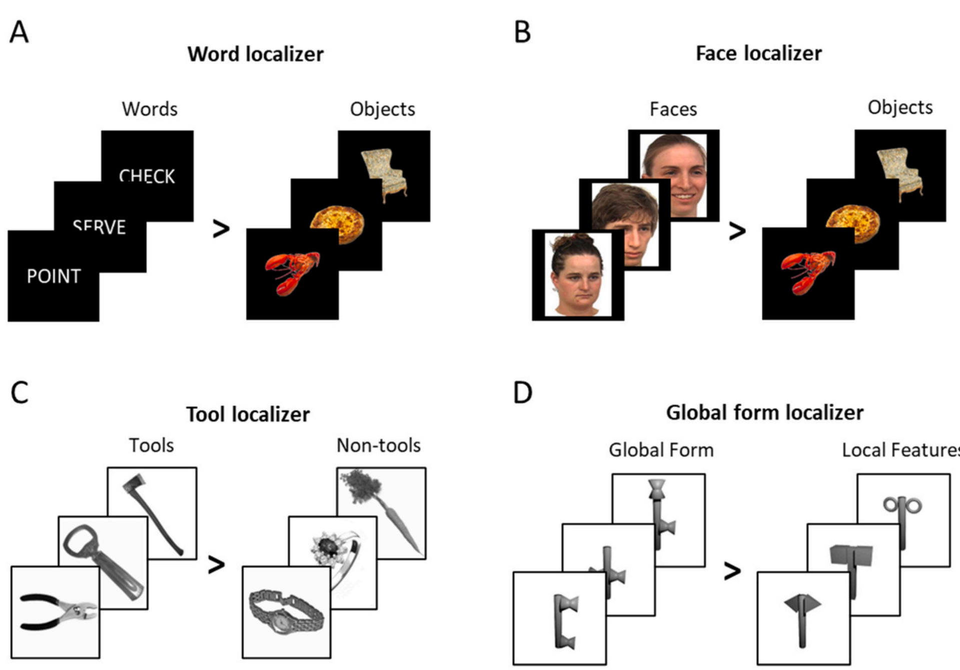

Fig. 2. Example stimuli from the (A) word, (B) face, (C) tool, and (D) global form localizers.

manipulated, but whose form is not directly related to their function (e.g., a carrot). Each condition was comprised of ten instances each of tools, non-tools, or scrambled object images (Chen et al., 2018; Chen et al., 2016). Each block contained 20 images, displaying each possible tool, non-tool, or scrambled image twice per block. All stimuli subtended ~6° visual angle on screen. Each image was presented for 700 ms with a 100 ms interstimulus interval (ISI) for a total of 16 s per block. The image order within the block was randomized. Participants also viewed blocks of fixation (16 s). Participants viewed 5 repetitions of each block per run, with blocks presented in a pseudorandom order under the constraint that all four block types (tool, non-tool, scrambled, fixation) were presented once before repetition. To maintain attention, participants performed an orthogonal one-back task, responding to the repetition of an image on consecutive presentations. Tool representations were measured as those voxels that responded more to the tool than the non-tool condition.

2.3.3. *Global form localizer*

On each run of the global form localizer (320 s), participants viewed blocks of object images in which either the spatial arrangement of component parts varied from image to image (global form condition), while the parts themselves stayed the same; or the features of the component parts varied from image to image (local feature condition), while the spatial arrangement of the parts stayed the same (Fig. 2D). Objects could have one of 10 possible spatial arrangements, and one of 10 possible part features. Spatial arrangements were selected to be qualitatively different from one another as outlined by the recognition-by-components (RBC) model (e.g., end-to-end; end-to-middle; Biederman, 1987). The component parts were comprised of qualitatively different features as outlined by the RBC model (e.g., sphere, cube). Because many dorsal regions are particularly sensitive to an object's orientation and axis of elongation (Sakata et al., 1998), all objects were presented in the same orientations and were organized around the same elongated segment, ensuring that they have identical principal axes. Stimuli subtended ~6° visual angle on screen.

Each block of the global form localizer contained 20 images, displaying each spatial arrangement or part feature twice per block depending on the condition. Each image was presented for 800 ms with a 200 ms interstimulus interval (ISI) for a total of 20 s per block. To minimize visual adaptation, the location of object images on the screen varied by ~2° every trial. The image order within the block was randomized. Participants also viewed blocks of a fixation cross (20 s). Participants viewed 5 repetitions of each block per run, with blocks presented in a pseudorandom order under the constraint that all three block types (relations, feature, fixation) were presented once before repetition. To maintain attention, participants performed an orthogonal one-back task, in which they responded via key press when detecting the repetition of an image on consecutive presentations. Global form representations were quantified as those voxels that responded more to the global form than the local feature condition.

2.4. *Statistical analysis*

Neural response. We first measured whether patients demonstrated any statistically reliable neural responses to the conditions of interest. We specifically created large ventral and dorsal region-of-interest (ROI) binary masks using probabilistic parcels (Julian et al., 2012; Wang et al., 2014) For the ventral visual pathway, we included parcels beginning at visual area 4 (V4) and ending at anterior portions of the fusiform, encompassing the typical positions of the word area, namely the VWFA, as well as face areas, namely the occipital face area (OFA) and FFA (see Supplemental Fig. 3). For the dorsal visual pathway, we included parcels beginning at visual area 3 A/B (V3A/B) and ending at intraparietal sulcus area 5 (IPS5) and the superior parietal lobe (SPL) (see Supplemental Fig. 3). Ventral and dorsal ROIs were purposefully created to encompass a large portion of cortex so as to accommodate patients' potentially altered anatomy and, thus, to ensure that we captured any statistically reliable neural responses in their ventral and dorsal pathways. However, an ROI-free analysis examining the entire hemisphere was also performed.

Because the patients' overall anatomy is altered due to their missing hemisphere, conventional registration techniques are not always successful. Thus, to register each ROI from MNI standard space to each individual patient, we first created a mirror symmetric version of each patient's brain by combining the anatomical image of the preserved hemisphere with a mirror-flipped version of the preserved hemisphere. We then computed the registration transformation between the MNI anatomical template and each patient's mirror symmetric anatomical image. This final transformation matrix was then used to register the ventral and dorsal ROIs to each patient's preserved hemisphere (i.e., their native anatomical space; see Supplemental Fig. 3). Ventral and dorsal registrations were manually inspected for each patient to ensure good alignment (see Supplemental Fig. 3). Control data were registered using standard procedures.

Neural responses within ventral and dorsal masks were measured as those voxels that survived a liberal uncorrected threshold of $p < .01$. We used a lax threshold because a relatively limited amount of data was collected for each participant (two runs per localizer), thereby limiting the statistical power. Moreover, because we were ultimately interested in comparisons between patient and control groups, it was primarily important that the same threshold was used for each participant. Results were qualitatively the same at higher thresholds, as well as when a threshold-free analysis was performed using all positive voxel values.

2.4.1. *Anatomical location*

To test whether the anatomical locations of responses within ventral and dorsal pathways aligned with those of controls, for each condition, we evaluated the distance between the peak response in the patients and the peak response in the controls.

To do so, we registered all participants (patients and controls) to MNI space and then computed the coordinate of the peak response to each condition within ventral and dorsal masks (ventral: words and face; dorsal: tools and global form). Because prior work has shown that the neural response to faces and global form (Ayzenberg and Behrmann, 2022b; Kamps et al., 2019) typically show both a posterior (faces: OFA; global form: posterior IPS) and anterior (faces: FFA; global form: anterior IPS) cluster, we further split the analysis for these conditions into posterior and anterior regions.

As there were relatively few patients compared to controls, we conducted our analyses on a patient-by-patient basis using non-parametric statistics. Specifically, for every condition (word, face, tool, global form), hemisphere (left, right), and region (ventral, dorsal), we computed bootstrapped 95% confidence intervals using the control data. On every resample of the data, 4 control participants (to match the number of patients with each hemisphere) were randomly selected (without replacement), and the mean Euclidean distance between their peak response for a condition and the remaining controls was calculated. This procedure was then repeated 10,000 times, thereby creating a distribution of distance values. We then tested whether the distance for each individual patient fell below the control distribution.

2.4.2. *Selectivity*

We measured whether patients exhibited normal levels of selectivity for each stimulus condition by computing the mean activation to each localizer contrast, the total active volume, and a composite score known as summed selectivity (Vin et al., 2023). Although mean activation and total active volume are common measures of selectivity, they only provide partial insight into the neural response profile for a given condition. For instance, the mean activation amplitude for the words > objects contrast may be normal for a patient relative to controls, but the patient may exhibit a much smaller area of activation compared to controls. By contrast, the overall area of activation in a patient may be comparable to that of controls, but mean activation may be overall lower. Summed selectivity sums each significant voxel value, thereby providing a holistic measure that captures both overall activation strength and the total active area.

For word and face conditions, we computed selectivity metrics within broad ventral binary masks (Julian et al., 2012; Wang et al., 2014) and selected those voxels that survived a liberal uncorrected threshold of $p < .01$. Similarly, for tools and global form, we computed selectivity metrics within broad dorsal binary masks (Wang et al., 2014) and selected those voxels that survived a liberal uncorrected threshold of $p < .01$. All selectivity metrics were analyzed in participants' native anatomical space.

Mean activation was computed as the mean of all standardized parameter estimate values (betas) above the threshold. Active volume (mm^3) was computed as a count of the total number of voxels above threshold. Finally, summed selectivity was computed by summing the standardized parameter estimate values for each surviving voxel. Because summed selectivity is influenced by the total number of voxels within a region and because participants have different sized brains, we normalized summed selectivity values for each condition by the total number of available voxels within each participants' ROI mask for that condition. For these values to be more easily interpretable, we rescaled them by a factor of 1000. As above, we conducted our analyses on a patient-by-patient basis using non-parametric statistics. Each patient's summed selectivity value was compared to bootstrapped 95% confidence intervals using the control data (10,000 resamples with replacement).

2.4.3. Decoding

Even if patients exhibited abnormal selectivity for each stimulus condition, the distributed pattern of their neural response may still potentially support encoding of each stimulus category. Thus, we also tested whether we could decode each stimulus condition from the patients' multivariate neural responses. Note, although a block-design is ideally suited to measure univariate selectivity for each condition, it is not well optimized for multivariate analyses. Thus, these analyses should be treated as exploratory.

We extracted the multivariate neural response (averaged across time) for each block of trials for a particular stimulus condition (word, face, tool, and global form extracted from blocks of each localizer) from each region (left, right hemisphere; ventral, dorsal pathway). Then, using a 30-fold cross-validation procedure, a Support Vector Machine (SVM) classifier was trained on the multivariate pattern for 80% of the blocks, and then tested on the held-out 20%. Decoding for each condition was tested against the multivariate neural response of its contrast (words vs. objects; faces vs. objects; tools vs. non-tools; global form vs. local features).

3. Results

3.1. Preliminary analyses

We first examined what proportion of control participants had significant activation to each condition (word, face, tool, global form) within each condition's preferred hemisphere (left, right) and ROI (ventral, dorsal). For ease of interpretation, the preferred hemisphere (left: L; right: R) and ROI (ventral: V; dorsal: D) for each condition is indicated as a subscript in the results: words_{LV}, faces_{RV}, tools_{LD}; global form_{RD}.

We found that the majority of control participants who completed the ventral localizer tasks exhibited significant activation to words_{LV} in their left VOTC (20/21 participants) and faces_{RV} in their right VOTC (20/21 participants). Similarly, every control participant who completed the dorsal localizer tasks exhibited significant activation to tools_{LD} in their left dorsal pathway (24/24) and global form_{RD} in their right dorsal pathway (24/24).

Next, we examined whether the number and location of significant clusters for each condition in the controls corresponded to their typical location based on the literature. Examination of the group activation maps in the ventral pathway revealed one posterior ROI in the ventral pathway for words_{LV}, corresponding to the VWFA (see Fig. 3A; Dehaene and Cohen, 2011) and two ROIs for faces_{RV} corresponding to OFA and FFA (see Fig. 3B; Kanwisher et al., 1997; Pitcher et al., 2011). In the dorsal pathway, we observed one anterior ROI for tools_{LD}, corresponding to the superior parietal lobule (see Fig. 3C; Johnson-Frey, 2004), and two ROIs for global form_{RD}, corresponding to posterior and anterior IPS (see Fig. 3D; Ayzenberg and Behrmann, 2022b).

We also tested whether control participants showed the predicted pattern of lateralization for each condition. In the ventral pathway, this analysis revealed stronger summed selectivity for words_{LV} in the left hemisphere compared to the right, $t(20) = 6.18$, $p < .001$, $d = 1.34$ and stronger summed selectivity for faces_{RV} in the right hemisphere compared to the left, $t(20) = 4.45$, $p < .001$, $d = 0.75$. Similarly, in the dorsal pathway, we found stronger summed selectivity for tools_{LD} in the left hemisphere compared to the right, $t(23) = 3.19$, $p = .004$, $d = 0.41$, and stronger summed selectivity to global form_{RD} in the right hemisphere compared to the left, $t(23) = 5.83$, $p < .001$, $d = 0.45$. These analyses replicate the previously reported response profiles for each condition in typical individuals (Ayzenberg and Behrmann, 2022b; Behrmann and Plaut, 2020; Garcea and Mahon, 2014).

Finally, we evaluated the relative strength of lateralization for each condition by examining how many control participants exhibited stronger responses in their preferred hemisphere for a condition than the group distribution in the non-preferred hemisphere. To this end, each control participant's summed selectivity for a condition in their preferred hemisphere was compared to bootstrapped control distribution of selectivity values (95% CIs) for that condition in the non-preferred hemisphere. As an example, each control participant's word_{LV} responses in their preferred left VOTC, was compared to the bootstrapped distribution of the word_{LV} responses for all controls in their non-preferred right VOTC.

This analysis revealed that the majority of participants (66.6%) exhibited significantly greater summed selectivity to words_{LV} in their preferred left hemisphere than the overall distribution of word_{LV} responses in the right hemisphere. However, for the other conditions, only a minority of participants exhibited significantly greater responses in the preferred hemisphere (faces_{RV}: 33.3%; tools_{LD}: 29.2%; global form_{RD}: 25.0%). Thus, although control participants, on the whole, exhibited a lateralization effect for each condition, the strength of lateralization in each individual participant's preferred hemisphere was rarely greater than the group distribution of responses in the non-preferred hemisphere.

3.2. Patient analyses

Our primary question of interest is whether functions that are typically activated to a greater extent in one hemisphere, as demonstrated in the control data, reorganize to the contralateral hemisphere following hemispherectomy. To this end, we focused on analyses comparing the response of each patient's intact, but 'non-preferred', hemisphere for each condition, to the 'preferred' (typical localization) hemisphere for each condition in controls. This comparison provides the necessary condition for determining whether a patient's intact hemisphere has adapted to be more like the controls' preferred hemisphere. The most critical comparisons are as follows:

Words: patient intact right ventral vs. control preferred left ventral
Faces: patient intact left ventral vs. control preferred right ventral
Tools: patient intact right dorsal vs. control preferred left dorsal
Global form: patient intact left dorsal vs. control preferred right dorsal

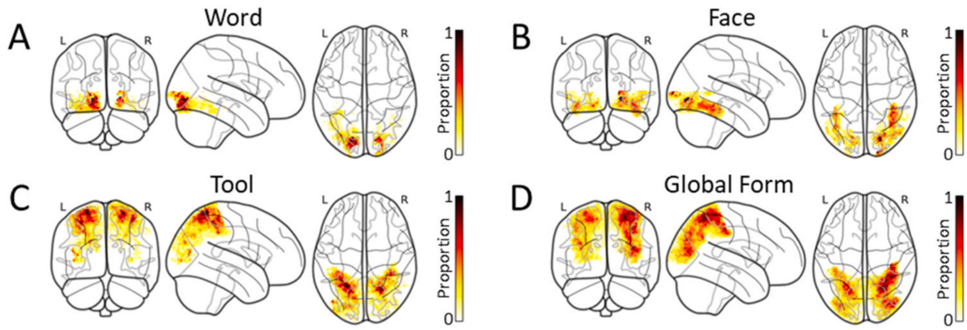

Fig. 3. Responses to (A) words$_{LV}$ and (B) faces$_{RV}$ in the ventral pathway, as well as (C) tools$_{LD}$ and (D) global form$_{RD}$ in the dorsal pathway of control participants. Voxel responses reflect the proportion of participants that had statistically significant responses within each pathway ($p < .01$; uncorrected). Figures are displayed on glass brains.

In addition to these comparisons, we also tested whether patient responses are stronger in their intact hemisphere than in the control's non-preferred hemisphere, and examined the extent to which patients whose preferred hemisphere for a condition is intact, exhibits a response that falls within the normal limit. For the results of every possible comparison, see Tables 2 and 3. As described in the methods, all patient metrics were compared to 95% CIs computed from a bootstrapped distribution of control participants. For the selectivity analyses, we focused on the summed selectivity metric as this provides an overall description of the response profile to a condition (see Methods). Moreover, we specifically tested whether patient responses were *below* the distribution of selectivity values for controls, because selectivity values within or above control distribution would be evidence of reorganization. For the specific percentiles of patients' responses relative to controls, see Table 3. All results are qualitatively similar when examining mean activation and total active volume (see Supplemental Figs. 4–5).

3.2.1. *Word representations*

In controls, words$_{LV}$ are represented more strongly in the left hemisphere of VOTC than the right hemisphere. Thus, we tested whether patients with a left hemispherectomy, and, therefore, only an intact right hemisphere, demonstrated normal word$_{LV}$ representations in their right hemisphere relative to controls' preferred left hemisphere (see Fig. 4).

We first examined whether patients showed any statistically reliable responses to words$_{LV}$ in their preserved right hemisphere. This analysis revealed that all four left hemispherectomy patients showed word$_{LV}$ responses in the posterior portion of their intact right VOTC (Fig. 4A-B). Next, we examined whether the location of peak responses to words$_{LV}$ in patients' intact hemisphere aligned with controls' peak responses in their preferred left hemisphere. This analysis revealed that none of the left hemispherectomy patients showed peak responses within the control distribution of distances (Fig. 4B).

Next, we examined whether the overall selectivity of word$_{LV}$ responses in patients was comparable to that of the controls' preferred left hemisphere. This analysis revealed that EB, KT, and FO's summed selectivity for words$_{LV}$ fell within the control distribution, whereas KN's did not (see Table 2 and Fig. 4C). Of these, EB and FO's responses were also greater than control's non-preferred right hemisphere, providing particularly strong evidence of reorganization in these patients. KT and KN's summed selectivity to words$_{LV}$ was comparable to control's non-preferred right hemisphere (see Table 3; and Fig. 4C).

Finally, given that word$_{LV}$ representations are typically lateralized to the left hemisphere, one might have also predicted that patients who have an intact left hemisphere would show normal word$_{LV}$ selectivity. Our results showed that only two of the four patients (patient SI and XC) with an intact left hemisphere showed summed selectivity that was comparable to that of controls left hemisphere, and, indeed, greater than control's non-preferred right hemisphere (see Table 3). One other patient (patient BN) showed summed selectivity that was comparable to control's non-preferred right hemisphere. Summed selectivity for the final patient (patient BI) was lower than both the left and right hemisphere of controls. Together, these analyses provide evidence that word$_{LV}$ representations do reorganize to the contralateral right hemisphere following left hemispherectomy, but also, offer some evidence that hemispherectomy disrupts the typical neural organization for the preserved hemisphere (see General Discussion).

3.2.2. *Face representations*

In controls, faces$_{RV}$ are represented more strongly in the right than left hemisphere of VOTC. Thus, we tested whether patients who have had a right hemispherectomy, and, therefore, have only an intact left hemisphere, demonstrated normal face$_{RV}$ representations in their left hemisphere as compared to controls' right hemisphere (see Fig. 5).

We first examined whether patients showed any statistically reliable responses to faces$_{RV}$ in their intact left VOTC. This analysis revealed that

Table 2
At-a-glance summary of selectivity results. Each row indicates whether a patient's summed selectivity score was below the control distribution (95% CIs; two-sided). Asterisks (*) indicate that the patient's score was *below* the control distribution, dashes (-) indicate that the patient's score was *inside* or *above* the control distribution. 'LH and 'RH' indicate whether the scores were compared to controls' left hemisphere or right hemisphere, respectively. The 'preferred' or typical hemisphere for each condition is underlined and in bold. For percentiles of each value, see Table 3.

Patient	Intact Hemisphere	Word		Face		Tool		Global Form	
		LH	RH	LH	**RH**	**LH**	RH	LH	**RH**
XC	Left	-	-	-	-	*	*	*	*
SI	Left	-	-	-	-	*	*	*	*
BI	Left	*	*	*	*	-	-	-	-
BN	Left	*	-	-	-	*	*	-	*
EB	Right	-	-	-	-	*	*	*	*
KT	Right	-	-	-	*	n/a	n/a	-	-
FO	Right	-	-	-	*	-	-	*	*
KN	Right	*	-	-	*	*	*	*	*

Table 3
A summary of selectivity percentiles for each patient. Each row indicates a patient's summed selectivity score as a percentile within the control distribution. Bold values indicate that the patient's score was significantly outside the control distribution, either *above* or *below* (95% CIs; two-sided). 'LH and 'RH' indicate whether the scores were compared to controls' left hemisphere or right hemisphere, respectively. The 'preferred' or typical hemisphere for each condition is underlined and in bold. Note, because two-sided comparisons were used, the threshold for significance is 2.5% and 97.5%, respectively.

Patient	Intact Hemisphere	Word		Face		Tool		Global Form	
		LH	RH	LH	**RH**	**LH**	RH	LH	**RH**
XC	Left	53.71	**99.99**	34.88	4.44	**1.03**	**2.29**	**0.11**	**0.00**
SI	Left	95.91	**100.00**	**99.99**	90.03	**0.28**	**0.09**	**0.00**	**0.0**
BI	Left	**0.00**	**0.01**	**0.28**	**0.04**	27.82	58.29	76.41	43.00
BN	Left	**0.49**	24.46	92.69	41.63	0.00	0.00	7.51	**0.43**
EB	Right	55.36	**99.99**	**98.95**	64.47	0.28	0.09	**0.53**	**0.01**
KT	Right	3.01	73.88	4.09	**0.28**	n/a	n/a	**99.97**	**99.60**
FO	Right	89.03	**100.00**	3.09	**0.25**	13.16	34.08	**0.00**	**0.00**
KN	Right	**1.48**	58.17	17.90	**1.49**	**1.01**	**1.94**	**0.00**	**0.00**

three out of four patients, (XC, SI, and BN), exhibited face$_{RV}$ responses in the posterior portion of their intact left VOTC, and all four patients, SI, BI, and BN, exhibited face$_{RV}$ responses in the anterior portion of their intact left VOTC (see Fig. 5A-B). Of these, SI and BN's peak responses aligned with the location of controls' peak voxel in posterior VOTC, and XC and BN's peak response to faces$_{RV}$ aligned with the location of controls in anterior VOTC (see Fig. 5B).

Next, we examined whether the overall selectivity of face responses in patients was comparable to controls' preferred right hemisphere. This analysis revealed that three out of four patients' (XC, SI, BN) summed selectivity for faces fell within the control distribution (see Table 2 and Fig. 5C). Of these, only patient SI showed face responses that were also significantly greater than control's non-preferred left hemisphere (see Table 3). Patient BI showed face responses in her intact left hemisphere that were lower than both left and right hemispheres of controls.

Next, given that face$_{RV}$ representations are typically lateralized to the right hemisphere, one might have also predicted that patients who have an intact right hemisphere would show normal face$_{RV}$ selectivity. Here, we found that only EB showed face$_{RV}$ responses that fell within the control distribution for face$_{RV}$ selectivity in the right hemisphere. However, the summed selectivity of the remaining three left hemispherectomy patients fell within the range of face responses in controls' non-preferred left hemisphere. These analyses show evidence that face$_{RV}$ representations reorganize to the contralateral hemisphere, and also suggest that hemispherectomy may disrupt the face$_{RV}$ representations in patient's preserved right hemisphere.

3.2.3. Tool representations

In controls, tools$_{LD}$ are represented more strongly in the left hemisphere of PPC than the right hemisphere. Thus, we tested whether patients who have had a left hemispherectomy, and therefore only have an intact right hemisphere, demonstrated normal tool$_{LD}$ representations in their right hemisphere as compared to control's left hemisphere (see Fig. 6).

We first examined whether patients showed any statistically reliable responses to tools in their intact right hemisphere. This analysis revealed that only FO and KN showed reliable tool$_{LD}$ responses in the anterior portion of their intact right dorsal pathway (Fig. 6A-B). Next, we examined whether the location of peak responses to tools in patients' intact hemisphere aligned with controls preferred left hemisphere. This analysis revealed that only KN showed peak responses within the control distribution (Fig. 6B).

Finally, we examined whether the overall selectivity of tool$_{LD}$ responses in patients was comparable to controls' preferred left hemisphere. This analysis revealed that only FO's summed selectivity for tools$_{LD}$ fell within the control distribution (see Table 2 and Fig. 6C), but did not surpass controls' tool responses in their non-preferred right hemisphere (see Table 3). Next, given that tool$_{LD}$ representations are typically lateralized to the left hemisphere, we tested whether patients who have an intact left hemisphere would show normal tool$_{LD}$ selectivity. However, our results showed that only BI's summed selectivity for tools fell within the control distribution. These analyses provide very little evidence that tool$_{LD}$ representations reorganize to the contralateral hemisphere, and further suggest that hemispherectomy may disrupt tool representations in patients with a preserved left hemisphere.

3.2.4. Global form representations

In controls, global form$_{RD}$ is represented more strongly in the right hemisphere of PPC than the left hemisphere. Thus, we tested whether patients who have had a right hemispherectomy, and therefore only have an intact left hemisphere, demonstrate normal global form$_{RD}$ representations in their left hemisphere as compared to control's preferred right hemisphere (see Fig. 7).

We first examined whether patients showed any statistically reliable responses to global form$_{RD}$ in their intact left PPC. This analysis revealed that three patients, XC, BI, and BN, exhibited global form$_{RD}$ responses in the posterior portion of their intact left PPC, and all four patients exhibited global form$_{RD}$ responses in the anterior portion of their intact left PPC (see Fig. 7A-b). Of these, BI and BN's peak responses aligned with the location of controls' peak responses in the posterior portions of their dorsal pathway, and XC and BI's peak responses aligned with controls in anterior portions of their dorsal pathway (see Fig. 7B).

Next, we examined whether the overall selectivity for global form$_{RD}$ in patients was comparable to controls. This analysis revealed that only BI's summed selectivity for global form$_{RD}$ fell within the control distribution (see Table 2 and Fig. 7C), but did not surpass the responses of control's non-preferred left hemisphere. Given that global form$_{RD}$ representations are typically lateralized to the right hemisphere, we tested whether patients who have an intact right hemisphere would show normal global form$_{RD}$ selectivity. Here we found that only KT showed global form$_{RD}$ responses that were comparable to controls, which, interestingly, surpassed both left and right hemispheres of controls (see Table 3 and Fig. 7C). These analyses show mixed evidence that global form$_{RD}$ representations reorganize to the contralateral hemisphere, and some evidence that hemispherectomy impairs the global form$_{RD}$ representation of the preserved right hemisphere.

3.2.5. Signal quality

One possible explanation for why patients did not show reorganization across both ventral and dorsal conditions is that they might have had excessive motion or poor temporal signal-to-noise ratio (tSNR). An analysis of patients' motion in the scanner revealed that all patients (and controls) exhibited less than 0.25° of rotation and less than 0.20 mm of translation within the scanner, well within the acceptable bounds for fMRI analyses (see Supplemental Fig. 6A-B). However, separate analyses of tSNR in ventral and dorsal pathways revealed that one patient's tSNR was lower than controls in the ventral pathway (patient FO) and two patients' tSNR was lower than controls in the dorsal pathway (patients KN and FO; see Supplemental Fig. 6C-D).

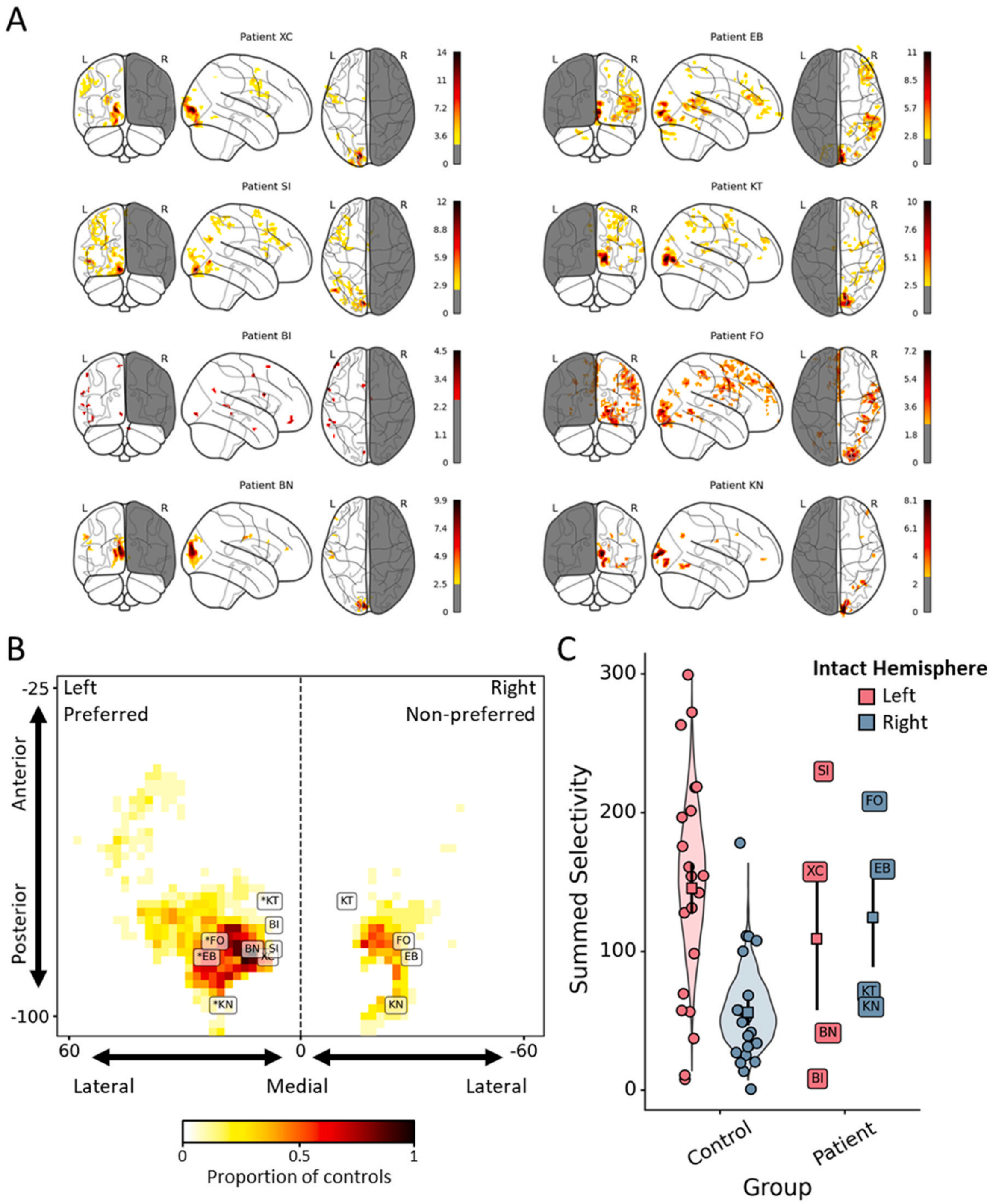

Fig. 4. Results from the word$_{LV}$ localizer. (A) Whole brain responses to words$_{LV}$ > objects in patients with intact left or right hemispheres displayed on a glass brain. (B) Visualization of word$_{LV}$ responses in controls and patients in the ventral pathway. The heatmap illustrates the 2D spatial distribution of group responses to words$_{LV}$ in controls, with darker colors indicating that a larger proportion of controls had significant activation at that coordinate. Each labeled point refers to the peak coordinate for a patient. Patients with an intact right hemisphere have been projected onto the preferred hemisphere of the map and are marked with an asterisk (*). (C) Summed selectivity for words$_{LV}$ in the ventral pathway. Violin plots depict the bootstrapped distribution of control participants' scores. Each unlabeled point refers to a single control participant's data, and each labeled point corresponds to a single patient. Small square symbols and error bars refer to the mean and standard error of each group, respectively.

Although two patients showed lower than average tSNR, these findings cannot explain the presence of reorganization in the ventral pathway, but not the dorsal pathway, for the remaining patients. Furthermore, individual patients' tSNR is largely inconsistent with their selectivity metrics. For instance, although FO was the only patient to show low tSNR for both ventral and dorsal pathways, she nevertheless showed evidence of reorganization for words$_{LV}$ in the ventral pathway, and was one of only two patients to show normal responses to tools$_{LD}$ in the dorsal pathway. By contrast, BI had the highest tSNR for the ventral pathway of all patients, and but showed little evidence of reorganization for words$_{LV}$ and faces$_{RV}$. Similarly, XC had the highest tSNR for the dorsal pathway, but showed little evidence of reorganization in the dorsal pathway. Overall, there does not seem to be a systematic relation between tSNR and reorganization, as there are patients with strong tSNR

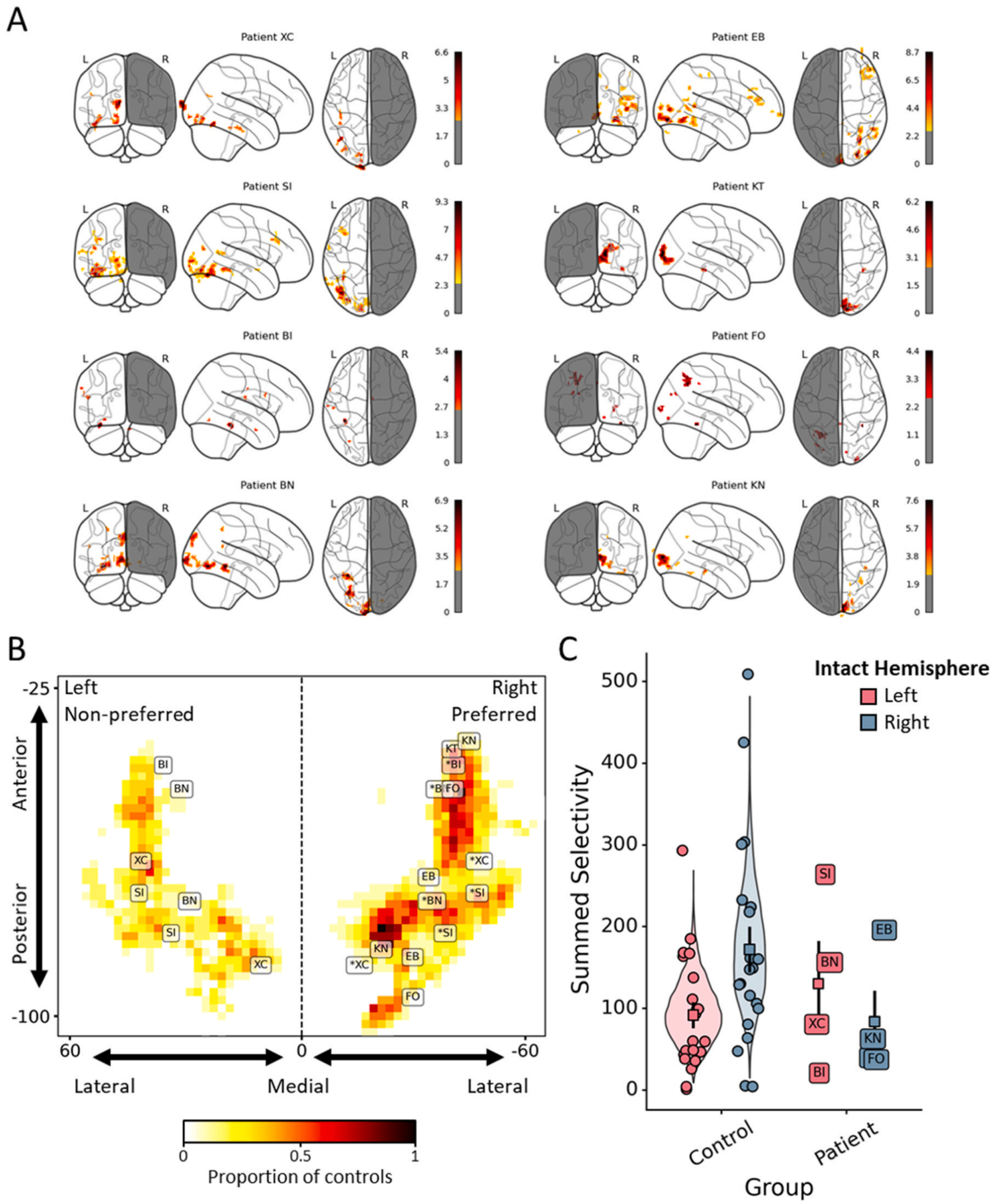

Fig. 5. Results from the face$_{RV}$ localizer. (A) Whole brain responses to faces$_{RV}$ > objects in patients with intact left or right hemispheres displayed on a glass brain. (B) Visualization of face$_{RV}$ responses in controls and patients in the ventral pathway. The heatmap illustrates the 2D spatial distribution of group responses to faces$_{RV}$ in controls, with darker colors indicating that a larger proportion of controls had significant activation at that coordinate. Each labeled point refers to the peak coordinate for a patient. Patients with an intact left hemisphere have been projected onto the preferred hemisphere of the map and are marked with a * . (C) Summed selectivity for faces$_{RV}$ in the ventral pathway. Violin plots depict the bootstrapped distribution of control participants' scores. Each unlabeled point refers to a single control participant's data, and each labeled point corresponds to a single patient. Small square symbols and error bars refer to the mean and standard error of each group, respectively.

in both pathways, but only evidence of reorganization in one (e.g., XC, EB, SI, BI). Finally, we would note that tSNR was overall higher in the dorsal pathway (M = 140.66, SD = 17.80) than the ventral pathway (M = 90.30, SD = 15.42) for both patients and controls ($p < .001$) and, thus, it is unlikely that signal quality can explain our results.

3.2.6. Age at surgery

One might also wonder whether the probability with which patients show reorganization is related to their age-at-time-of-surgery. Although we do not have a sufficient sample size to conduct correlation analyses between age and selectivity metrics, qualitative analysis of our results suggests that there is no systematic relation between age-at-time-of-surgery and the probability of reorganization. For instance, both XC

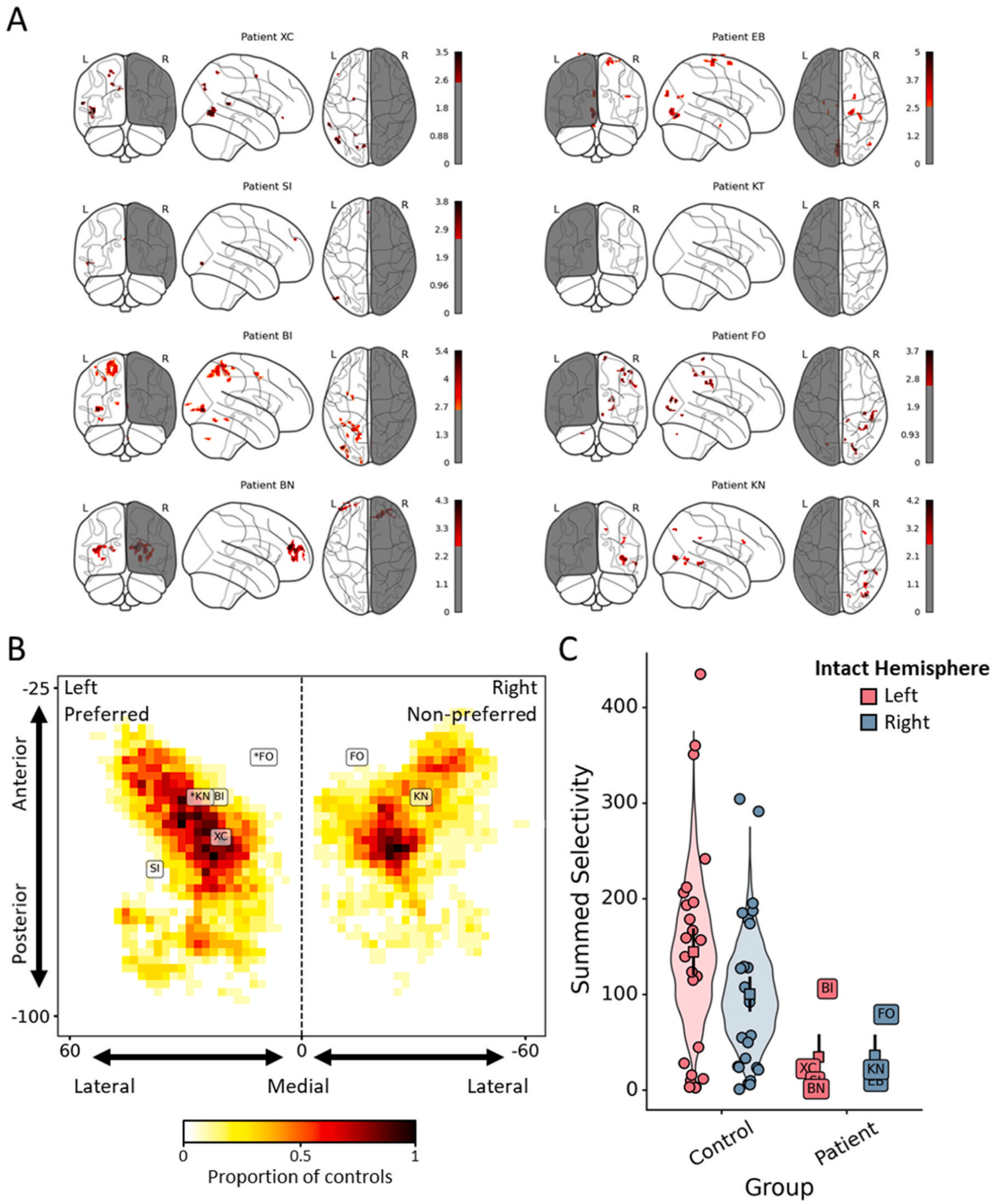

Fig. 6. Results from the tool$_{LD}$ localizer. (A) Whole brain responses to tools$_{LD}$ > non-tools in patients with intact left or right hemispheres displayed on a glass brain. (B) Visualization of tool responses in controls and patients in the dorsal pathway. The heatmap illustrates the 2D spatial distribution of group responses to tools$_{LD}$ in controls, with darker colors indicating that a larger proportion of controls had significant activation at that coordinate. Each labeled point refers to the peak coordinate for a patient. Patients with an intact right hemisphere have been projected onto the preferred hemisphere of the map and are marked with a * . (C) Summed selectivity for tools$_{LD}$ in the dorsal pathway. Violin plots depict the bootstrapped distribution of control participants' scores. Each unlabeled point refers to a single control participant's data, and each labeled point corresponds to a single patient. Small square symbols and error bars refer to the mean and standard error of each group, respectively.

and SI showed evidence of reorganization in the ventral pathway, but not the dorsal pathway, even though XC was the youngest patient at the time of surgery (1.0 year) and SI was the second oldest (11 years). By contrast, BI and KT were the only two patients to show normal responses for global form$_{RD}$ in the dorsal pathway, even though BI was one of the youngest patients at the time of surgery (1.3 years) and KT was the oldest (13 years). Thus, there is no clear relation between age-at-the-time of surgery and the propensity for either pathway to reorganize.

3.2.7. Summary

Overall, we found greater evidence of functional reorganization in the ventral pathway compared to the dorsal pathway. In the ventral pathway, six out of eight patients showed comparable summed selectivity in their intact hemisphere on par with control's preferred

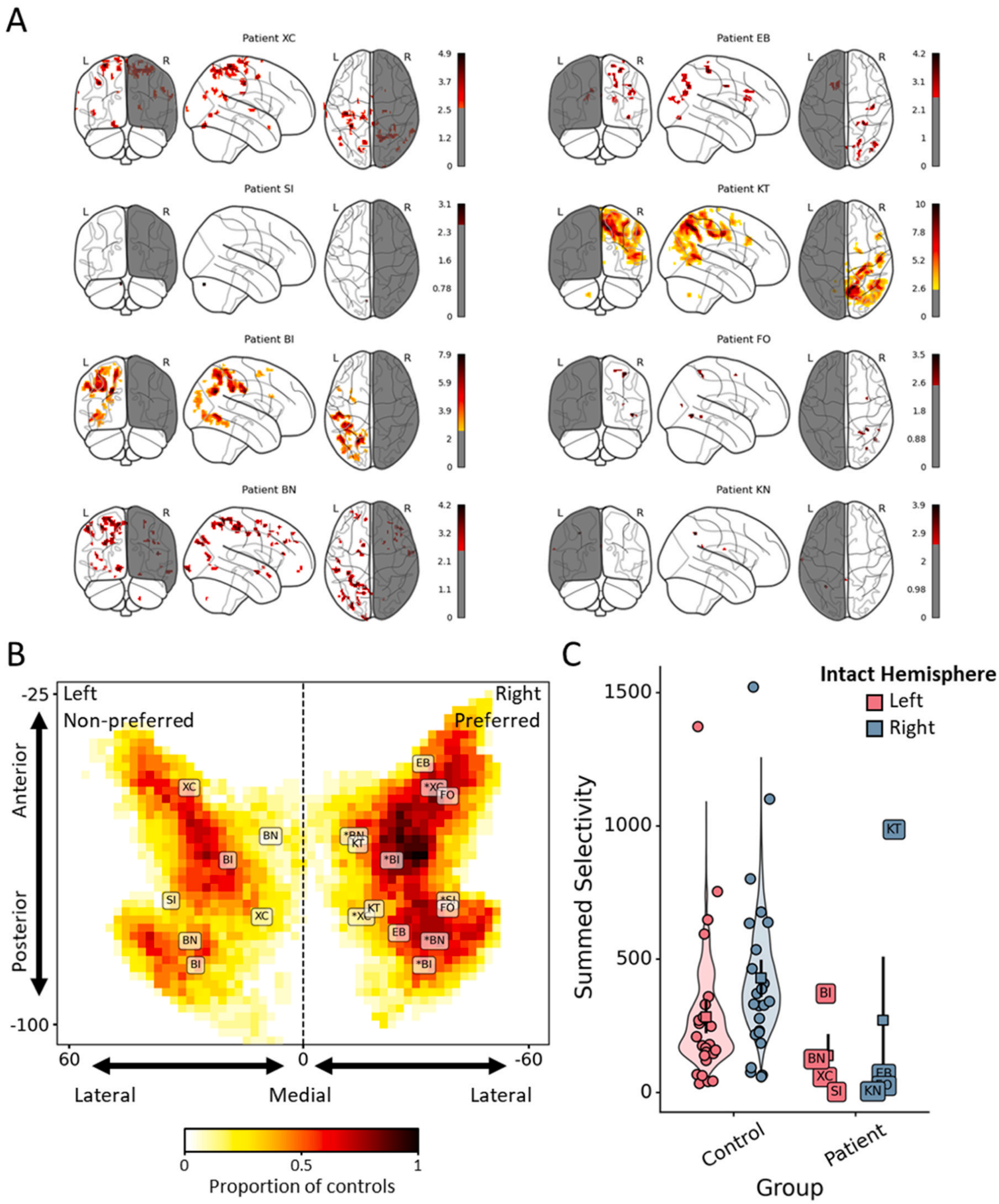

Fig. 7. Results from the global $form_{RD}$ localizer. (A) Whole brain responses to global $form_{RD}$ > local features in patients with intact left or right hemispheres displayed on a glass brain. (B) Visualization of global $form_{RD}$ responses in controls and patients in the dorsal pathway. The heatmap illustrates the 2D spatial distribution of group responses to global $form_{RD}$ in controls, with darker colors indicating that a larger proportion of controls had significant activation at that coordinate. Each labeled point refers to the peak coordinate for a patient. Patients with an intact left hemisphere have been projected onto the preferred hemisphere of the map and are marked with a * . (C) Summed selectivity for global form in the dorsal pathway. Violin plots depict the bootstrapped distribution of control participants' scores. Each unlabeled point refers to a single control participant's data, and each labeled point corresponds to a single patient. Small square symbols and error bars refer to the mean and standard error of each group, respectively.

contralateral hemisphere (3/4 for $words_{LV}$; 3/4 for $faces_{RV}$), with every patient showing at least some activation in their preserved hemisphere. By contrast, a smaller proportion of patients showed reorganization in the dorsal pathway, with only two patients showing comparable summed selectivity to controls preferred contralateral hemisphere (1/3 $tools_{LD}$; 1/4 global $form_{RD}$).

However, we also found a number of inconsistencies, such that the preferred representation of patients' intact hemisphere was often below the control distribution for a condition's preferred ipsilateral hemisphere. Even across these inconsistencies, we found that the representations of patient's ventral pathway were generally comparable to at least one hemisphere of controls, with 7 out of 8 patients showing comparable summed selectivity to controls for both $words_{LV}$ and $faces_{RV}$. By contrast, only 2 out of 7 and 3 out of 8 showed any comparable summed selectivity for $tools_{LD}$ and global $form_{RD}$, respectively (see Table 2). Altogether, these findings provide evidence that the ventral pathway is better able to reorganize following functional hemispherectomy than the dorsal pathway, but also that hemispherectomy may impact the preferred representations of the intact hemisphere.

3.3. Distributed representations

Although patients showed little evidence of reorganization in the dorsal pathway, patients also generally showed little impairment on recognition processes linked to the dorsal pathway such as $tool_{LD}$ use or shape perception. Moreover, not all patients showed normal selectivity to $words_{LV}$ and $faces_{RV}$, and yet demonstrate strong performance on word and face perception tasks (Granovetter et al., 2022). In the absence of normal univariate selectivity, how might patients accomplish these feats? One possibility is that the representations for each of these properties is distributed.

In the sections that follow, we provide two tests of this hypothesis, first, by examining whether summed selectivity in patients' entire hemisphere, rather than in circumscribed regions, is comparable to controls, and second, by testing whether each condition can be decoded using the multivariate pattern of neural responses in ventral and dorsal pathways.

3.3.1. Hemisphere analyses

We analyzed whether participants' summed selectivity for each condition across their entire hemisphere is comparable to controls' summed selectivity in the preferred hemisphere. As in previous analyses, because we are most interested in examining reorganization, we focus our analyses on comparisons between each patients' preserved hemisphere and the preferred hemisphere for a condition in controls (words: patient right vs. control left; faces: patient left vs. control right; tools: patient right vs. control left; global form: patient left vs. control right). For the results of all patients see Supplemental Table 1.

For the ventral conditions, we found that all four patients with a preserved right hemisphere exhibited normal or high summed selectivity for $words_{LV}$ (see Fig. 8A), and only two patients with a preserved left hemisphere (patients SI and BN) exhibited normal summed

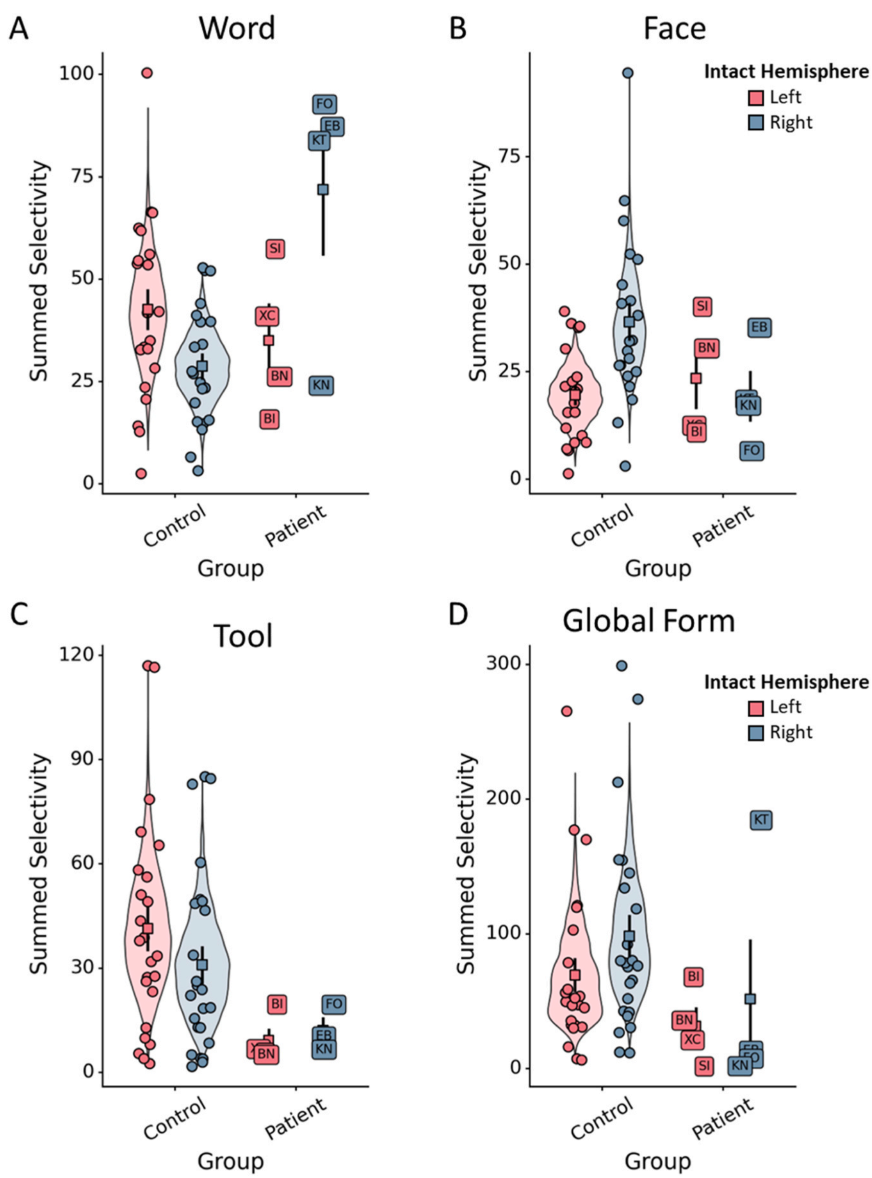

Fig. 8. Whole-brain summed selectivity results for (A) $words_{LV}$, (B) $faces_{RV}$, (C) $tools_{LD}$, and (D) global $form_{RD}$ in patients and controls. Violin plots depict the bootstrapped distribution of control participants' scores. Each unlabeled point refers to a single control participant's data, and each labeled point corresponds to a single patient. Small square symbols and error bars refer to the mean and standard error of each group, respectively.

selectivity for faces$_{RV}$ (see Fig. 8B). Interestingly, however, the word$_{LV}$ responses of EB, KT, and FO, who had a preserved right hemisphere, surpassed those of the controls. For the dorsal conditions, we found that only FO exhibited normal summed selectivity for tools$_{LD}$ in their preserved right hemisphere (see Fig. 8C), and only BI exhibited normal summed selectivity for global form$_{RD}$ in their preserved left hemisphere (see Fig. 8D). Thus, the overall pattern of summed selectivity across the entire hemisphere was comparable to that revealed by the analyses restricted to just ventral and dorsal pathways.

3.3.2. Multivariate decoding

Next, we analyzed how well we could decode each condition of interest relative to its localizer contrast (words vs. objects; faces vs. objects; tools vs. non-tools; global form vs. local features). Here, again, we are most interested in examining reorganization, and so we focused our analyses on comparisons between each patients' preserved hemisphere and the preferred hemisphere for a condition in controls (words: patient right vs. control left; faces: patient left vs. control right; tools: patient right vs. left; global form: patient left vs. control right). For the results of all patients see Supplemental Table 2.

For the ventral conditions, we found that three of four intact right hemisphere patients exhibited normal decoding accuracy for words$_{LV}$, and three of four intact left hemisphere patients exhibited normal decoding for faces$_{RV}$. For the dorsal conditions, we found that two intact right hemisphere patients (out of three), EB and KN, exhibited normal decoding for tools$_{LD}$, and three out of four intact left hemisphere patients exhibited normal decoding for global form$_{RD}$. Altogether, these findings suggest that the multivariate response for each condition could theoretically support patients' behavioral performance. It is important note, however, that the current experimental design, using blocked conditions, is not optimized for multivariate decoding, and thus these analyses should be treated as exploratory and interpreted with caution.

3.3.3. Summary

Overall, our analysis of the distributed pattern of responses across the entire hemisphere mirrored the region-of-interest analyses described previously. As in the first section, a greater number of patients showed normal summed selectivity in their intact hemisphere for ventral conditions (3/4 for words$_{LV}$; 2/4 for faces$_{RV}$) than for dorsal conditions (1/3 for tools$_{LD}$; 1/4 for global form$_{RD}$). Our decoding analyses largely mirrored these findings for the ventral pathway, with similar proportions of patients' decoding accuracy being comparable to controls

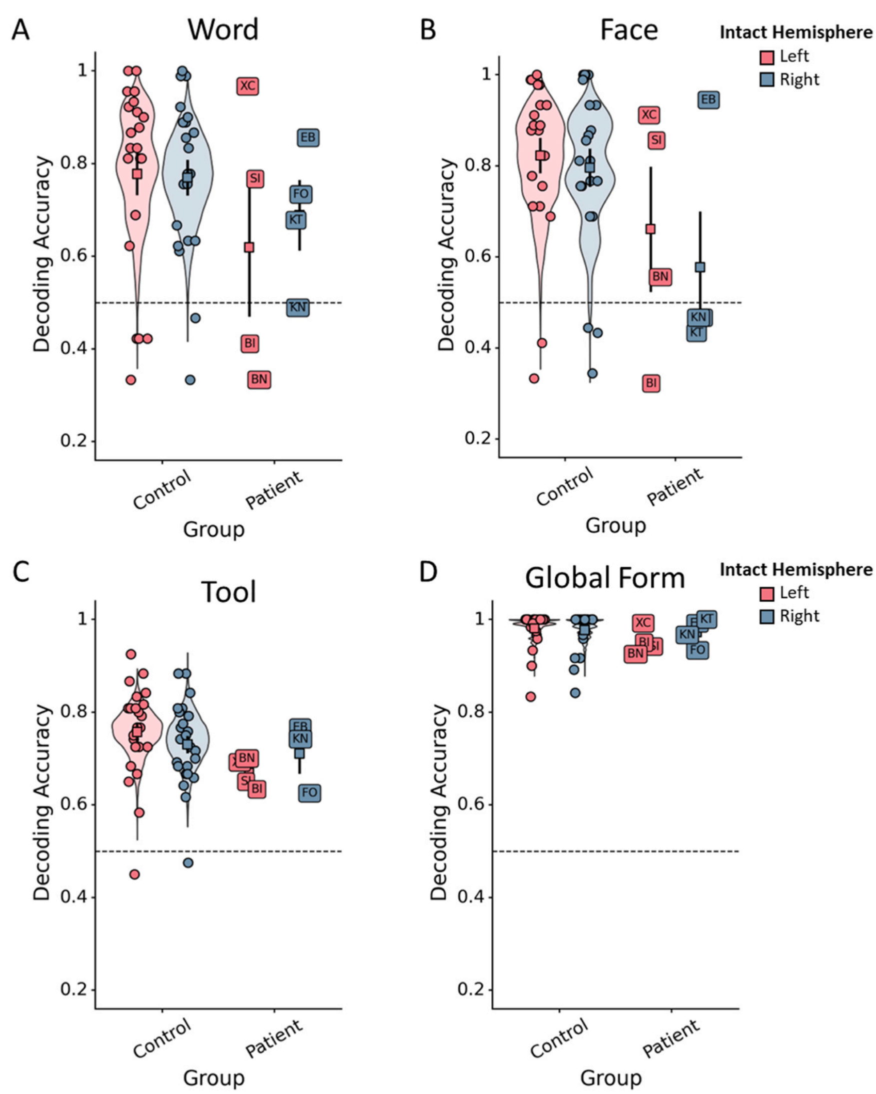

Fig. 9. Decoding accuracy for (A) words$_{LV}$ vs. objects, (B) faces$_{RV}$ vs. objects, (C) tools$_{LD}$ vs. non-tools, and (D) global form$_{RD}$ vs. local features in each patient and control's intact hemisphere. Violin plots depict the bootstrapped distribution of control participants' scores. Each unlabeled point refers to a single control participant's data, and each labeled point corresponds to a single patient. Small square symbols and error bars refer to the mean and standard error of each group, respectively.

(3/4 for words$_{LV}$; 2/4 for faces$_{RV}$). However, in the dorsal pathway, we found that a larger proportion of patients showed comparable decoding accuracy than selectivity (2/3 for tools$_{LD}$; 3/4 for global form$_{RD}$). Thus, although the dorsal pathway showed little evidence of functional reorganization when only the univariate signal was examined, the distributed pattern of dorsal responses may be sufficient to support tool and global form perception.

3.4. General discussion

In the current study, we sought to understand the capacity of ventral and dorsal visual pathways to functionally reorganize following a large-scale surgical resection, namely, hemispherectomy. The hypothesis was that, if the dorsal pathway matures earlier than the ventral pathway, then, following hemispherectomy, it may be less plastic and malleable, and, therefore, less able to reorganize than the ventral pathway. To test this hypothesis, we conducted fMRI scans of an equal number of left and right hemispherectomy patients while they completed localizer tasks designed to elicit lateralized responses in the left or right hemisphere of ventral or dorsal pathways. Overall, we found that a greater number of patients showed reorganization in the ventral pathway than the dorsal pathway. Importantly, because we examined ventral and dorsal reorganization in the same individual patients, these results cannot be explained by between-subjects factors such as disease etiology, age of surgery, and age at the time of testing. Together, these findings suggest that the dorsal pathway may develop earlier and exhibit a smaller window of plasticity.

Overall, six out of eight patients showed evidence of reorganization in the ventral pathway – three out of four for words and three out of four for faces. By contrast, only two patients showed reorganization in the dorsal pathway – one patient for tools (patient FO) and one for global form (patient BI), regardless of whether the analyses were restricted to ROIs or the entire hemisphere. These findings are consistent with the only other known study that compared reorganization of ventral and dorsal functions, in a patient with resections to both pathways (Ahmad et al., 2022), and provides support for our initial hypothesis that the dorsal pathway may be less able to reorganize potentially because it matures earlier than the ventral pathway.

How do we reconcile these results with prior studies that have examined neural and behavioral recovery of perceptual functions following damage or resection? As described in the introduction, previous work has found evidence that the functions of the ventral pathway reorganize following VOTC resections (Liu et al., 2019; Liu et al., 2018), and that hemispherectomy patients retain a high degree of word and face recognition performance (Granovetter et al., 2022). However, it is important to note that not all patients in these studies showed evidence of reorganization (Liu et al., 2019). In fact, studies find mixed evidence of functional reorganization across the literature. For instance, many studies find no evidence of recovery of ventral functions, such as word and face recognition, following damage in childhood (Farah et al., 2000; Hadjikhani and de Gelder, 2002), even when the damage occurred on day 1 of life. By contrast, other studies find successful reorganization and normal recognition performance (Cohen et al., 2004; Mancini et al., 1994), even when the disruptions occurred late in childhood (for review, see Liu and Behrmann, 2017; Vargha-Khadem and Polkey, 1992).

Although age at time-of-surgery is typically thought to be an important factor in determining the degree to which brain areas are able to reorganize, our results and the extant literature, suggest that this is not the case. Specifically, we did not find a systematic relation between age-at-surgery and the likelihood that the ventral pathway reorganizes in an individual, such that even patients who had surgery at 13-years-age showed evidence of reorganization in the ventral pathway. One possible explanation is that the brain remains relatively malleable until (at least) late adolescence. Indeed, studies have, surprisingly, found few relations between age-at-surgery and cognitive outcomes (for review, see Van Schooneveld and Braun, 2013), including performance on face and word tasks in a large sample of hemispherectomy patients (Granovetter et al., 2022). However, another possibility is that epilepsy itself may serve as the trigger for reorganization. That is, the preserved hemisphere of patients may already have begun to reorganize before surgery as a way compensate for the dysfunctional epileptic hemisphere. In this view, reorganization in the intact ventral pathway may have started well in advance of the surgery. To dissociate these possibilities, future studies will need to be conducted with larger sample sizes so that the precise relation between age-of-disruption and reorganization can be measured, and longitudinal studies of change would offer important insights, as well. Studies of patients with more diverse disease etiology might also shed light on this issue.

However, one important, but not universal, factor that seems to impact reorganization in previous studies is whether children experience unilateral or bilateral damage. On the whole, patients seem more likely to show neural reorganization and recovery of function if only one hemisphere is damaged, theoretically because the other hemisphere is able to compensate (Liu and Behrmann, 2017). Our results align with this literature on ventral pathway reorganization. We found that the majority, but not all, patients with hemispherectomy showed reorganization of function to their contralateral hemisphere in their ventral pathway. Given that only one hemisphere was resected, their intact hemisphere was available to compensate for the damage.

It is less clear, however, why patients showed abnormal responses to conditions that should already be lateralized to the intact hemisphere. For instance, only two patients with an intact left hemisphere showed normal word responses, and only one patient with an intact right hemisphere showed normal face responses. One possibility is that reorganization in the ventral pathway causes 'neural crowding' or competition between representations (Danguecan and Smith, 2019; Lidzba et al., 2006). For example, the presence of word representation in the right hemisphere encroaches on regions that would normally be exclusively face-selective, and vice versa for the presence of face representations in the left hemisphere. Indeed, prior work has shown that a patient with reorganization of words to their right hemisphere also had smaller than normal face ROIs (Liu et al., 2018), and over typical development, the emergence of VWFA in children correlates with an increasingly smaller face response in the left hemisphere (Behrmann and Plaut, 2020; Dehaene, 2005; Dundas et al., 2013; Nordt et al., 2021). However, it is important to note, that, although only a few patients showed normal selectivity for the preferred condition in their preserved hemisphere, almost all patients (7 out of 8) showed ventral responses that were consistent with at least one hemisphere of controls.

Although, for the ventral pathway, we found that the majority of hemispherectomy patients showed selectivity comparable to the preferred hemisphere of controls, these values did not always exceed controls' non-preferred hemisphere. This finding naturally raises the question of whether our findings point to reorganization in the ventral pathway, as we have argued, or simply 'normal' unimpaired processing. This question is challenging to address because even individual control participants rarely showed responses in their preferred hemisphere that were greater than the group distribution of all control responses for the non-preferred hemisphere (see Preliminary Analyses). However, our patient results overall aligned with control data in this context. Specifically, a majority of control participants showed stronger selectivity to words in their preferred left hemisphere than the distribution of values for the non-preferred right hemisphere. This finding is mirrored by the fact that 2 left hemispherectomy patients showed both a normal response relative to control's preferred left hemisphere, as well as stronger responses than controls' non-preferred right hemisphere. For faces, only a minority of control participants showed stronger responses in the preferred right hemisphere for faces than the group distribution in the non-preferred left hemisphere. Similarly, only one patient showed selectivity for faces that was both comparable to controls' preferred right hemisphere, and greater than controls' non-preferred left hemisphere for faces. Thus, these findings suggest that, at minimum, patients showed evidence of reorganization for words, and that the overall selectivity for words and faces was comparable to controls. However, regardless of whether patients' data is better described as reorganization and/or spared processing in the ventral pathway, our results suggest a developmental distinction between ventral and dorsal pathways. Indeed, few patients showed responses in the dorsal pathway that were comparable to either hemisphere of controls. Thus, these findings continue to suggest that the dorsal pathway is more vulnerable to damage than the ventral pathway because it is earlier to mature.

There are far fewer studies examining the organization of the dorsal pathway following damage in childhood, with most focusing on processes related to visually guided action. Yet, action-related processes may be less likely to reorganize following damage given the strong one-to-one anatomical mapping between motor movements and the contralateral hemisphere (Schieber, 2001). Here, we examined perceptual processes of the dorsal pathway, namely tool and global form representations, and found little evidence that these functions reorganize to their contralateral homologue. These findings are consistent with the hypothesis that the dorsal pathway matures early, and therefore has a smaller window of plasticity relative to the ventral pathway. Moreover, these findings align broadly with the 'dorsal vulnerability hypothesis' (Braddick et al., 2003), which posits that the dorsal pathway is particularly sensitive to disruption in childhood. Indeed, studies have shown widespread deficiencies in perceptual processes linked to the dorsal pathway in developmental disorders like Cortical (or Cerebral) Visual Impairment or William's syndrome (Grinter et al., 2010; Macintyre-Béon et al., 2010). Children with these disorders rarely recover normal perceptual abilities. However, it is important to acknowledge that direct comparisons between our results and these disorders are challenging because, unlike disruptions from surgery or injury, these disorders also cause persistent bilateral, brain-wide effects that may not be solely linked to the dorsal pathway.

It is interesting to note that the only two patients to show normal responses to global form in the dorsal pathway (patient BI and KT), are also the only patients who did not undergo a full anatomical hemispherectomy (see Table 1), and have some spared parietal tissue in their disrupted hemisphere. Although we did not observe any responses in their disrupted hemisphere (see Fig. 7A), it is nevertheless possible that this spared tissue supports normal representations in their fully intact hemisphere. Indeed, BI is the only patient to show normal responses for both tools and global form in the dorsal pathway. Interestingly, she is also the only patient who does not show any normal responses in her ventral pathway. However, this pattern is less consistent for tool responses, such that only patient FO demonstrated evidence of reorganization for tools, and, unfortunately, data on tools were not available for KT.

A final, and related, puzzle from our work is how hemispherectomy patients maintain relatively accurate behavioral performance despite some patients showing abnormal selectivity in ventral and dorsal pathways. Indeed, all of the hemispherectomy patients tested are able to read and write (albeit, to a greater or lesser extent), and show reasonably good performance on word, face, and shape recognition tasks (see Methods and Supplemental Materials). One explanation is that some degree of neural response for each condition is sufficient, though not optimal, to support a base rate of behavioral performance. Indeed, although no patient showed normal selectivity across all the conditions tested, almost all patients showed at least some activation to each localizer, with many also showing above chance multivariate decoding – particularly in the dorsal pathway. However, another possibility is that patients have learned alternative strategies to accomplish these tasks, that do not rely on the same mechanisms as controls. Although we examined patients' overall accuracy on face, word, and object recognition tasks, future work is needed explore exactly *how* patients succeed at these tasks.

There are, however, a number of limitations with the current study. First, given the unique nature of this population, the number of participants is small and it is generally difficult to attain large samples of hemispherectomy patients. Indeed, the majority of the existing hemispherectomy studies report findings from just one or two patients (e.g., Patterson et al., 1989). This limited our ability to interpret the relation between reorganization and factors such as age-of-surgery, as well as to evaluate fully the degree to which MRI signal metrics may have affected our measurements. Moreover, due to timing constraints with each patient, we were only able to collect a limited amount of data per patient, which further limited signal-to-noise metrics for each condition. Nevertheless, a fundamental strength of the current design is that we were able to compare reorganization of ventral and dorsal pathways in the very same patients, thereby ruling out many of these patient specific factors in explaining the difference between ventral and dorsal pathways.

In conclusion, we sought to provide a detailed exploration of the capacity of ventral and dorsal pathways to reorganize following large-scale resections and to shed light on the possible developmental trajectories of each pathway. Using a within-subjects design, we found greater evidence of reorganization for the ventral pathway than the dorsal pathway, consistent with the claim that the ventral pathway matures later and has an extended window of plasticity, compared with the dorsal pathway. However, we also found evidence that hemispherectomy may disrupt preferred representations in patients' anatomically-preserved hemisphere (perhaps as a result of neural crowding), which makes drawing overarching conclusions about the nature of neural reorganization in the visual system challenging. To successfully characterize the processes that drive functional reorganization, future research must use larger sample sizes and collect larger amounts of data per patient, so as to better relate patient-specific factors to neural processes. Nevertheless, our results provide insight into the nature of plasticity across different brain areas, and the developmental trajectories of ventral and dorsal pathways.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Marlene Behrmann reports financial support was provided by National Institutes of Health.

Data availability

All processed data and analysis code can be found at: https://github.com/vayzenb/ventral-dorsal-reorganization.git.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.dcn.2023.101323.

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