With Childhood Hemispherectomy, One Hemisphere Can Support—But is Suboptimal for—Word and Face Recognition

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Abstract

The left and right cerebral hemispheres are important for word and face recognition, respectively—a specialization that emerges over human development. But children who have undergone a hemispherectomy develop with only one hemisphere. The question is whether this preserved hemisphere, be it left or right, can support both word and face recognition. Here, a large sample of patients with childhood hemispherectomy and age-matched controls performed word- and face-matching tasks. Controls viewed stimuli either in one visual field (restricting initial processing to one hemisphere) or, like the patients, in central vision. Across word and face tasks, patients performed comparably to controls using primarily one hemisphere, but more poorly than controls viewing stimuli centrally with both hemispheres engaged. Additionally, patients showed deficits in low-level visual processing that may explain their word/face recognition deficits relative to controls. Altogether, the findings suggest that either hemisphere alone can support word and face recognition, albeit sub-optimally.

Introduction

The visual perception of complex patterns, such as words and faces, is governed by the ventral visual pathway (Barttfeld et al., 2018; Grill-Spector and Malach, 2004; Grill-Spector and Weiner, 2014). Here, word and face recognition is largely, albeit not solely, the product of computations in the left and right hemispheres (LH and RH), respectively (Behrmann and Plaut, 2020, 2015). This hemispheric superiority profile is well-supported by behavioral (Dundas et al., 2013), electrophysiological (Dundas et al., 2014; Maurer et al., 2008; Rossion et al., 2003), and neuroimaging (Dehaene et al., 2002; Hasson et al., 2002; Puce et al., 1996) investigations. Neuropsychological studies in adults further suggest that each hemisphere is necessary for one of the two processes: whereas adults with focal lesions in left ventral occipitotemporal cortex (VOTC) show specific, significant impairments in word reading (Behrmann et al., 1990; Cohen et al., 2003; Damasio and Damasio, 1983), those with focal lesions in right VOTC show specific, significant impairments in face recognition (Albonico and Barton, 2019; De Renzi, 1986; Landis et al., 1986). That these striking impairments arise from focal lesions lends credence to the claim of hemispheric superiorities for word and face recognition, at least in the adult human brain (Robotham and Starrfelt, 2017).

Unlike these adult lesion patients, however, *children* who undergo resection of an entire cerebral hemisphere, or hemispherectomy (also hemispherotomy; see Kim et al. (2018) for distinction), for pharmacoresistant epilepsy treatment can show remarkable maintenance and/or recovery of cognitive functions post-surgery (Moletto et al., 2018; Pulsifer et al., 2004; van Empelen et al., 2004). It is established that hemispheric superiorities for word and face recognition emerge over development and with experience (Dehaene et al., 2010; Scherf et al., 2007). It is less clear, however, whether there is sufficient plasticity such that development with a single hemisphere can normatively support both word and face recognition. A further question to be answered is whether this plasticity is equivalent for the left and right hemispheres, or whether the integrity of both word and face recognition is contingent on *which* of the two

hemispheres is ultimately preserved. The answers to these questions have the potential to shed light on proposed foundational qualities of the computational profiles of each of the hemispheres.

In addition to the hemispheric superiorities for complex visual patterns, there are hemispheric superiorities for low-level visual information. Several behavioral and neuroimaging studies have confirmed that the left hemisphere (LH) is better tuned for high spatial frequency (HSF) information, which is well suited for detecting fine edges and abrupt luminance changes. In contrast, the right hemisphere (RH) is better tuned for low spatial frequency (LSF) information with fewer transitions between an image's darker and lighter patches such that global shape may still be derived (Hellige et al., 2010; Kauffmann et al., 2014; Sergent and Hellige, 1986). Indeed, on behavioral experiments, adults show respective LH and RH advantages for classifying HSF and LSF stimuli (Kitterle et al., 1992; Kitterle and Selig, 1991; Peyrin et al., 2003). Consistently, on functional magnetic resonance imaging (fMRI), the LH and RH show greater selectivity for HSF and LSF gratings, respectively (Peyrin et al., 2004). Further confirmation comes from studies with patients with LH or RH lesions who show respective deficits in processing HSF or LSF input (dos Santos et al., 2013). The differential tuning of the LH and RH for HSF and LSF stimulus identification, respectively, is well aligned with hemispheric superiorities for words and faces: words consist of greater power in the HSF interval, whereas faces are characterized by a broad band of HSFs and LSFs. In fact, on fMRI, word- and face-selective voxels evince respective selectivity for HSF and LSF gratings (Woodhead et al., 2011), and a posterior LH lesion results in both reduced HSF sensitivity and impaired reading (alexia; Roberts et al., 2013). One possible mechanism whereby a single hemisphere can support both word and face recognition may be atypical sensitivity to select SF ranges. Either preserved hemisphere, be it the LH or RH (or perhaps only one of these), may, for example, have an atypically broad SF profile and, in this way, accommodate both word and face recognition.

Thus, the primary objectives of the current study were to determine: 1) whether pediatric patients who develop with only one hemisphere exhibit comparable word and face recognition to age-matched typically developing controls, 2) whether performance is contingent on which hemisphere is preserved, and 3) whether patients' SF tuning profile of the preserved hemisphere differs from the corresponding hemisphere of controls. That is, despite hemispheric biases that emerge in typical development (Behrmann and Plaut, 2020, 2015), can one hemisphere (either left or right) normatively support both word and face recognition, and is this contingent on the individual's SF tuning profile?

Results

Hemispherectomy patients (here and throughout, the term includes hemispherotomy patients) performed word/face discrimination and SF identification tasks (see Materials and Methods and Figures 1 and 3 for details) with stimuli presented foveally in central vision. To examine the competence of a patient's single hemisphere, their performance was compared to that of the "*one-hemisphere controls"* who viewed stimuli on separate trials in the LVF or RVF in order to restrict initial processing to one hemisphere (Bourne, 2006). As patients viewed stimuli centrally while one-hemisphere controls viewed stimuli in the half-fields, to equate viewing conditions to the patients, a second group, the *"central controls"* viewed stimuli under conditions identical to those of the patients. Whilst equating fixation conditions here and ensuring more similar foveal acuity for the patients and controls, this manipulation resulted in a difference in hemispheres available for processing (one for patients, two for central controls). This "confound," however, turns out to be a feature rather than a bug in that it permits a direct comparison between the capabilities of a single hemisphere (in patients) and central controls for whom visual information is encoded by both hemispheres. It should be noted that one-hemisphere controls were not directly compared to central controls because the two groups

differed on two variables: the stimuli's foveal representation and the number of hemispheres primarily utilized for the tasks.

Twenty-six hemispherectomy patients, 17 with left-sided resections and 9 with right-sided resections; 93 one-hemisphere controls; and 34 central controls participated in at least one of the experimental tasks (word recognition, face recognition, SF identification). For a detailed patient summary, sample sizes of each group for each task, and description of age-matching, see Materials and Methods. Accuracy (the proportion of correct trials) was used as the primary dependent variable, as reaction time (RT) may be confounded by significant motor impairments (including with hand movements) among the patients (Kim et al., 2018; van Empelen et al., 2004). In fact, RT has been shown to be longer in cases with larger lesions (Heitzer et al., 2019). For reference, RT data are plotted in Fig. S1 and S2.

In the following group analyses, an α criterion of 0.05 was designated as the significance threshold. Additionally, an effect size (Cohen's *d*) of less than 0.35, between 0.35 and 0.65, and greater than 0.65 should be interpreted as small, moderate, and large, respectively (Sawilowsky, 2009). Last, to confirm null hypotheses (or lack thereof) Bayes Factors (BFs) were computed as the ratio of the prior predictive probabilities of the null model excluding the effect of interest and interactions of that effect with other predictors, to the full alternative model. A BF between 0.33 and 1, 0.1 and 0.33, 0.03 and 0.1, 0.01 and 0.03, or less than 0.01 should be interpreted as anecdotal, moderate, strong, very strong, or extreme evidence for the *alternative* model, respectively. On the other hand, a BF between 1 and 3, 3 and 10, 10 and 30, 30 and 100, or greater than 100 should be interpreted as anecdotal, moderate, strong, very strong, or extreme evidence for the *null* model, respectively (Lee and Wagenmakers, 2013; Wagenmakers, 2007). See Materials and Methods for further details on statistical computations.

<u>Word and Face Discrimination</u>

Participants viewed sequential pairs of stimuli (words and faces, in separate blocks) and indicated via one of two key presses whether stimuli in a pair were the same or different (Fig. 1). All patients and central controls viewed all stimuli at central fixation (Fig. 1A). In contrast, for one-hemisphere controls, the second stimulus in a pair was presented in the LVF or RVF (randomly, approximately half of trials for each field; Fig. 1B) with brief exposure duration to preclude saccades. Thus, word and face discrimination performance accuracy could be compared between patients with only a single hemisphere vs. each one-hemisphere controls and central controls using both hemispheres.

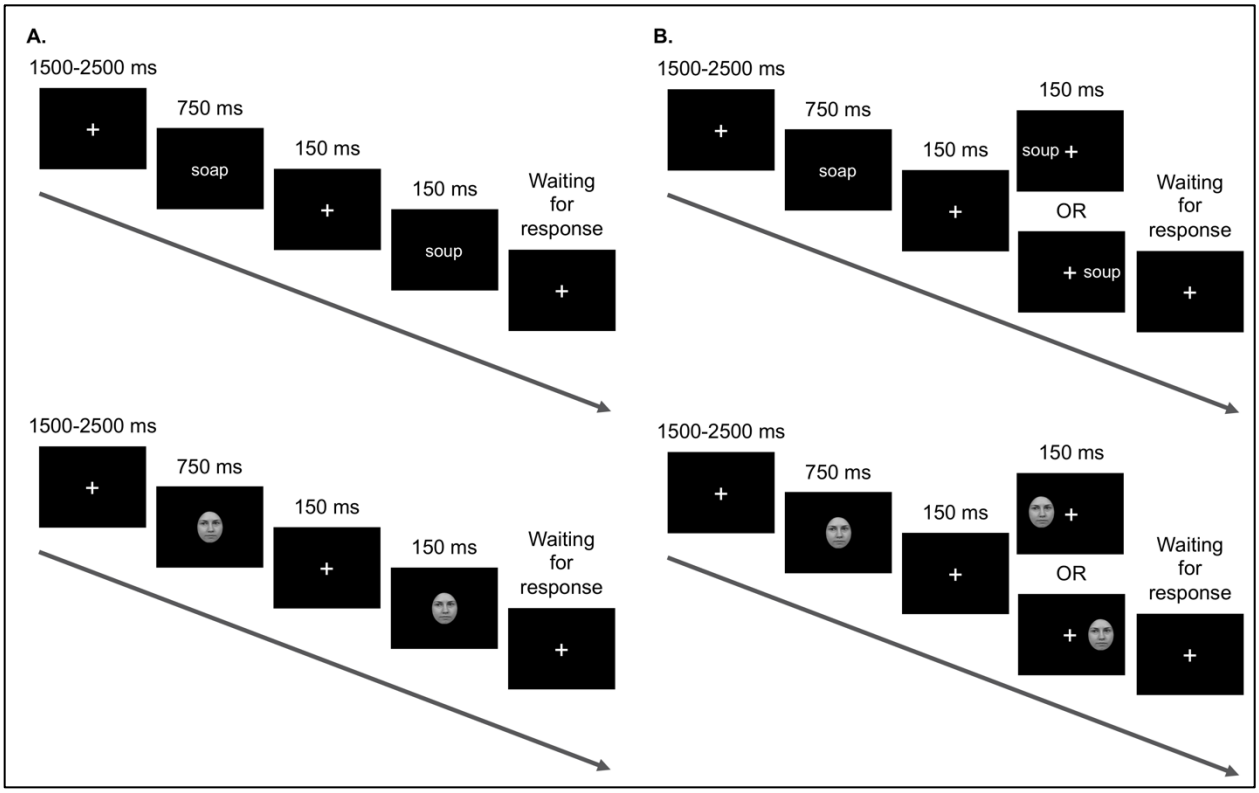

Figure 1. Participants viewed sequential pairs of words (top) and faces (bottom) in separate blocks. Participants were asked to indicate, via a key press, whether stimuli in a pair were the same or different. Stimuli are not drawn to scale. **A**: Patients and "central controls" viewed all stimuli at central fixation. **B**: "One-hemisphere controls" viewed the second stimulus in one of two visual hemifields on a given trial to initially restrict processing to a single hemisphere (Bourne, 2006).

For each group comparison (patients vs. one-hemisphere controls and patients vs. central controls), a linear mixed effects model was fit to the data (plotted in Fig. 2). Group (patients vs. controls), primary hemisphere used (left vs. right; patients' preserved hemisphere or controls' hemisphere associated with a hemifield), stimulus category (words vs. faces), and

all interactions between these variables were modeled as predictors of accuracy. Note that hemisphere used was not modeled as a predictor for the patients vs. central controls comparison as, in this instance, hemisphere used (one vs. two) is equivalent to group. Age was also included in the models as a covariate predictor, as evidence suggests that hemispheric biases for word and face recognition change over development (Behrmann and Plaut, 2020; Dehaene-Lambertz et al., 2018; Dundas et al., 2014). Participant was the sole random effect term in each model, with a different intercept for each participant. The predictions for the group comparisons are laid out below.

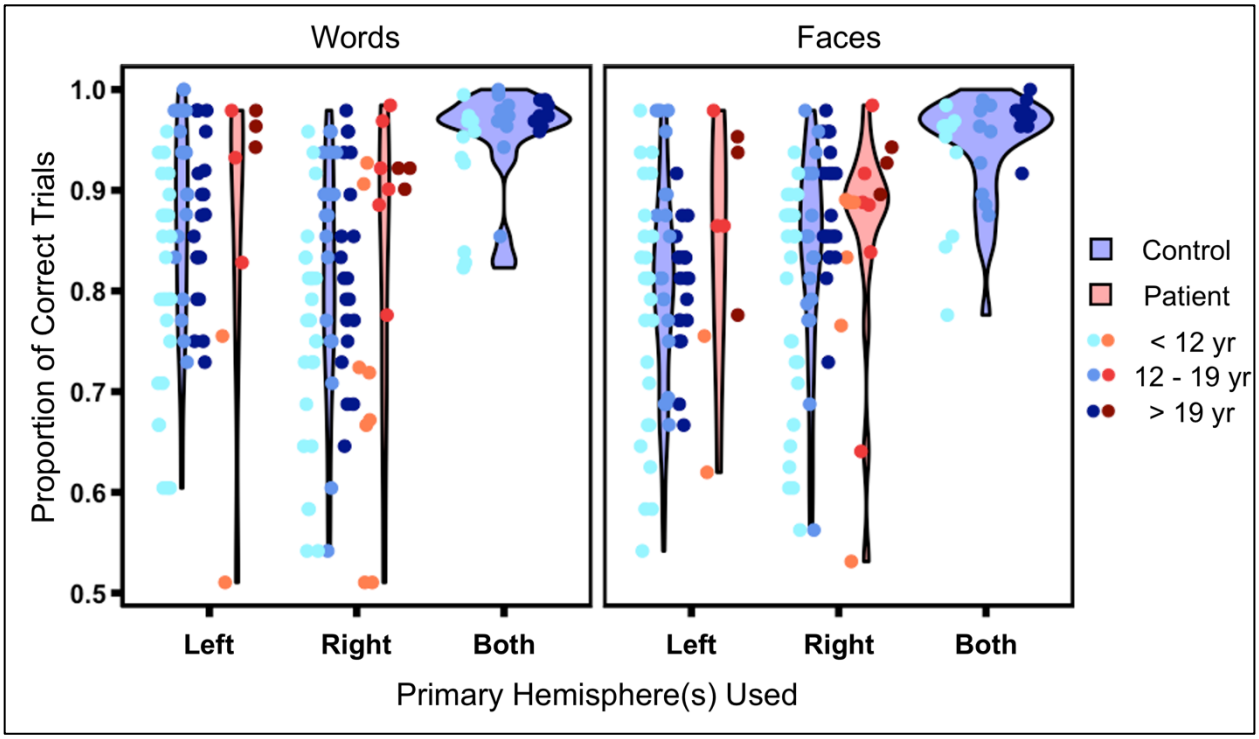

Figure 2. Violin plots show the distribution of accuracy values on the word and face recognition tasks for each group (patients and controls) by hemisphere used (left vs. right for patients and "one-hemisphere" controls viewing stimuli in the hemifields; both hemispheres for "central controls" viewing stimuli centrally) and stimulus category (words vs. faces). Overlaid point plots show the individual values for each participant. To visualize any effect of age, points are separated by terciles of the age distribution, shown in different shades of blue (controls) and red (patients). Points are randomly jittered to minimize overlapping data. yr = years.

Patients vs. One-Hemisphere Controls

If hemispheric biases for stimulus categories differed by group (for example, if patients with only a RH were to perform poorly on face or on word recognition relative to controls), a

significant three-way interaction of group x hemisphere used x stimulus category on accuracy would be expected. As this three-way interaction is most important, it is discussed first followed by lower-order interactions, and then main effects. Critically, there was no such significant interaction ($t_{(223)} = 0.54$, $p = 0.59$, $d = 0.04$, BF = $1.53*10^{1}$; see Fig. 2). At the same time, there was a significant two-way interaction effect of hemisphere used x stimulus category on accuracy ($t_{(223)} = 4.52$, $p < 0.01$, $d = 0.30$, BF = $8.57*10^{-3}$), suggesting that the well-established hemispheric superiorities for words and faces (Behrmann and Plaut, 2020, 2015) held equivalently over group. In fact, the two-way interaction effects of group x hemisphere used ($t_{(220)} = 0.34$, $p = 0.73$, $d = 0.02$, BF = $2.71*10^{2}$) and group x stimulus category ($t_{(223)} = 0.86$, $p = 0.39$, $d = 0.06$, BF = $2.10*10^{2}$) on accuracy were not significant. Strikingly and most importantly, patients and controls performed comparably to one another across tasks: there was no significant main effect of group on accuracy ($t_{(197)} = 0.75$, $p = 0.45$, $d = 0.05$, BF = $5.77*10^{4}$). Moreover, there was, as might be expected, a significantly positive main effect of age on accuracy ($t_{(95)} = 4.42$, $p < 0.01$, $d = 0.45$, BF = $2.39*10^{-3}$).

Further analyses were conducted as, in the analysis above, hemisphere used is a within-subjects measure for controls (because they view stimuli separately in either hemifield) but a between-subjects measure for patients (because each patient has only one hemisphere). Furthermore, it is necessary to examine the effect of stimulus category separately for each hemisphere given the significant hemisphere used x stimulus category interaction. Thus, linear mixed effects models were fit separately for each hemisphere to determine the predictive effects of group, stimulus category, and their interaction on accuracy. Age and participant were modeled as a covariate and random effect, respectively, as before. Consistent with the findings above, the groups performed comparably to one another across tasks: there was no significant main effect of group on accuracy when using either the LH ($t_{(123)} = 0.83$, $p = 0.41$, $d = 0.07$, BF = $9.30*10^{1}$) or RH ($t_{(147)} = 0.46$, $p = 0.64$, $d = 0.04$, BF = $1.49*10^{2}$). Additionally, there was no significant group x stimulus category interaction effect on accuracy for either the LH ($t_{(74)} = 0.86$,

192 $p = 0.39$, $d = 0.10$, BF = 8.44) or RH ($t_{(83)} = 0.23$, $p = 0.82$, $d = 0.03$, BF = $1.25*10^{1}$). Notably, as
193 expected, there were significant main effects of stimulus category on accuracy for each the LH
194 and RH, with greater accuracy for the LH on words than faces ($t_{(74)} = 3.95$, $p < 0.01$, $d = 0.46$,
195 BF = $1.14*10^{-1}$), and for the RH, on faces than words ($t_{(83)} = 2.17$, $p = 0.03$, $d = 0.24$, BF = 7.03).
196 These findings are consistent with the well-established LH and RH superiority for words and
197 faces, respectively (Behrmann and Plaut, 2020, 2015). Last, as before, there was a significantly
198 positive main effect of age on accuracy for each the LH ($t_{(74)} = 3.09$, $p < 0.01$, $d = 0.36$, BF =
199 $1.38*10^{-1}$) and RH ($t_{(83)} = 4.13$, $p < 0.01$, $d = 0.45$, BF = $5.44*10^{-3}$), consistent with the age-
200 related effect across development, as noted above.

201 Thus far, there is a clear absence of a group difference, independent of hemisphere
202 used and stimulus category. Nevertheless, to obtain further substantiation that the patients'
203 performance did not differ from that of the controls, the profiles of individual patients relative to
204 one-hemisphere controls were examined further. Each patient's accuracy was compared to the
205 distribution of accuracy of controls (while adjusting for age as a covariate), a common practice
206 for detecting deficits of neuropsychology cases (see Materials and Methods for details;
207 Crawford et al., 2011; Crawford and Garthwaite, 2012; Crawford and Howell, 1998). No patient,
208 regardless of the side of resection, showed a deficit on either task compared to controls
209 primarily using each their LH and RH (first two rows of Table 1), further confirmation that the two
210 groups showed comparable performance to one another on the word and face recognition
211 tasks.

Table 1. Individual patient accuracy on the word and face recognition tasks compared to distributions of controls using primarily the LH, RH, or both hemispheres. Each cell shows the percentage of patients in each group who showed an accuracy deficit compared to a given control distribution. Rows indicate the control distribution of comparison, and columns indicate the patient group and stimulus category.

	Patients with LH		**Patients with RH**	
	Words	**Faces**	**Words**	**Faces**
Controls Using Primarily LH	0%	0%	0%	0%
Controls Using Primarily RH	0%	0%	0%	0%
Controls Using Both Hemispheres	37.50%	42.86%	41.18%	25.00%

Altogether, these results provide evidence that patients with only a single hemisphere performed as well on both word and face recognition as controls using primarily a single hemisphere. Intriguingly, this was independent of the hemisphere resected. Importantly, independent of group, there appeared to be LH and RH advantages for word and face accuracy, respectively, as would be expected based on known hemispheric superiorities for the two visual categories (Behrmann and Plaut, 2020, 2015). Last, that no individual patients exhibited deficits on either task relative to controls, provides further confirmation of the similarities in word and face recognition between the groups.

Patients vs. Central Controls Using Both Hemispheres

In contrast to the patient vs. one-hemisphere control comparison, which showed comparable between-group accuracy across tasks, central controls outperformed patients on both word and face recognition: there was a significant main effect of group on accuracy ($t_{(101)}$ = 4.27, $p < 0.01$, $d = 0.42$, BF = $5.27*10^{-5}$; see Fig. 2 for the central control data under “both hemispheres”) that was not qualified by stimulus category. That is, there was no significant interaction effect of group x stimulus category on accuracy ($t_{(56)}$ =1.08 , $p = 0.29$, $d = 0.14$, BF = 5.94), suggesting patients’ relatively lower accuracy compared to controls’ was independent of the task. Additionally, there was no significant main effect of stimulus category on accuracy ($t_{(56)}$

= 0.44, p = 0.66, d = 0.06, BF = $5.85*10^{1}$). Last, as might be expected, there was a significantly positive main effect of age on accuracy ($t_{(56)}$ = 4.41, p < 0.01, d = 0.59, BF = $2.50*10^{-3}$).

To evaluate whether patients' accuracies differed from central controls' as a function of the side of resection, separate linear mixed effects models were fit for patients with only a LH and those with only a RH. Group, stimulus category, and their interaction were modeled as predictors of accuracy, with age and participant modeled again as a covariate and random effect, respectively. Consistent with the findings above, independent of the side of resection, patients had significantly lower accuracy than controls across both tasks: there was a significant main effect of group on accuracy when using either the LH ($t_{(54)}$ = 4.10, p < 0.01, d = 0.56, BF = $3.85*10^{-2}$) or RH ($t_{(93)}$ = 3.91, p < 0.01, d = 0.41, BF = $1.19*10^{-5}$), again not qualified by stimulus category. That is, there was no significant group x stimulus category interaction effect on accuracy when using either the LH ($t_{(39)}$ = 0.45, p = 0.65, d = 0.07, BF = 7.98) or RH ($t_{(48)}$ = 1.55, p = 0.13, d = 0.22, BF = 3.04). There also was no significant main effect of stimulus category on accuracy when using either the LH ($t_{(39)}$ = 0.81, p = 0.42, d = 0.13, BF = $3.73*10^{1}$) or RH ($t_{(48)}$ = 0.43, p = 0.67, d = 0.06, BF = $2.50*10^{1}$), as before. Last, as above, there was a significantly positive main effect of age on accuracy when using either the LH ($t_{(39)}$ = 3.47, p < 0.01, d = 0.56, BF = $4.65*10^{-2}$) or RH ($t_{(48)}$ = 4.01, p < 0.01, d = 0.58, BF = $9.68*10^{-3}$).

To again examine the individual patients' profiles, each patient's accuracy was compared to the distribution of accuracy of central controls. Proportions of patients with deficits (ranging from 25 to 43%) relative to central controls are reported in the last row of Table 1 and are largely consistent with the inferential analyses, with many patients falling outside the distribution of central controls.

Altogether, these results suggest that, independent of the side of resection, and even with central fixation equated, patients with a single hemisphere showed significantly lower accuracy on word and face recognition compared to controls using both hemispheres. This

group difference is in clear contrast with the comparison of patients to controls using primarily one hemisphere, where there were no between-group differences on either task.

Spatial Frequency Identification

Some researchers attribute the hemispheric biases for word and face recognition in the typically developing brain to differential SF tuning of the two hemispheres (Brederoo et al., 2020; Hsiao and Lam, 2013; Woodhead et al., 2011). This raises the question of whether SF tuning differs in patients who develop both word and face recognition within a single hemisphere. To assess this, Gabor patches (sinusoidal gratings) of either 6 cycles per degree (cpd; HSF) or 1.5 cpd (LSF; randomly, approximately half of trials for each) were presented to participants who reported whether gratings were perceived as “narrow” (HSF) or “wide” (LSF). This approach (rather than establishing thresholds) was deemed to be feasible for younger children and has proved successful for children in previous work (Ossowski & Behrmann, 2015). As before, patients viewed stimuli at central fixation (Fig. 3A). One-hemisphere controls viewed stimuli either in the LVF or RVF (randomly, approximately half of trials for each; Fig. 3B), while central controls viewed stimuli at fixation (as in Fig. 3A).

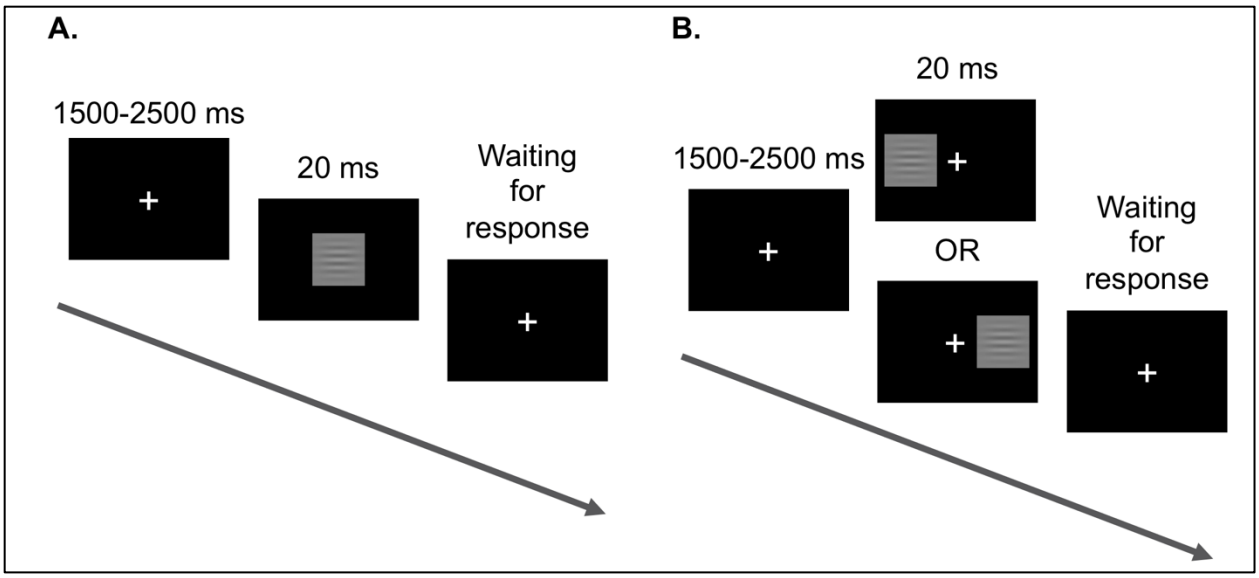

Figure 3. Participants viewed sequential presentations of Gabor patches (sinusoidal gratings). Participants were asked to indicate, via a key press, whether a patch had narrow or wide stripes/lines. Stimuli are not drawn to scale. **A**: Patients and "central controls" viewed all stimuli at central fixation. **B**: "One-hemisphere controls" viewed all stimuli in one of two visual hemifields on a given trial to initially restrict processing to a single hemisphere (Bourne, 2006).

As with the word and face discrimination tasks, for each group comparison (patients vs. one-hemisphere controls and patients vs. central controls), a linear mixed effects model was fit to the data (plotted in Fig. 4). Group (patients vs. controls), primary hemisphere used (left vs. right), stimulus category (HSF vs. LSF), and all interactions between these variables were modeled as predictors of accuracy. As hemisphere used is equivalent to group for the patients vs. central controls comparison, no separate factor of hemisphere was included. As before, age and participant were modeled as a covariate and random effect, respectively.

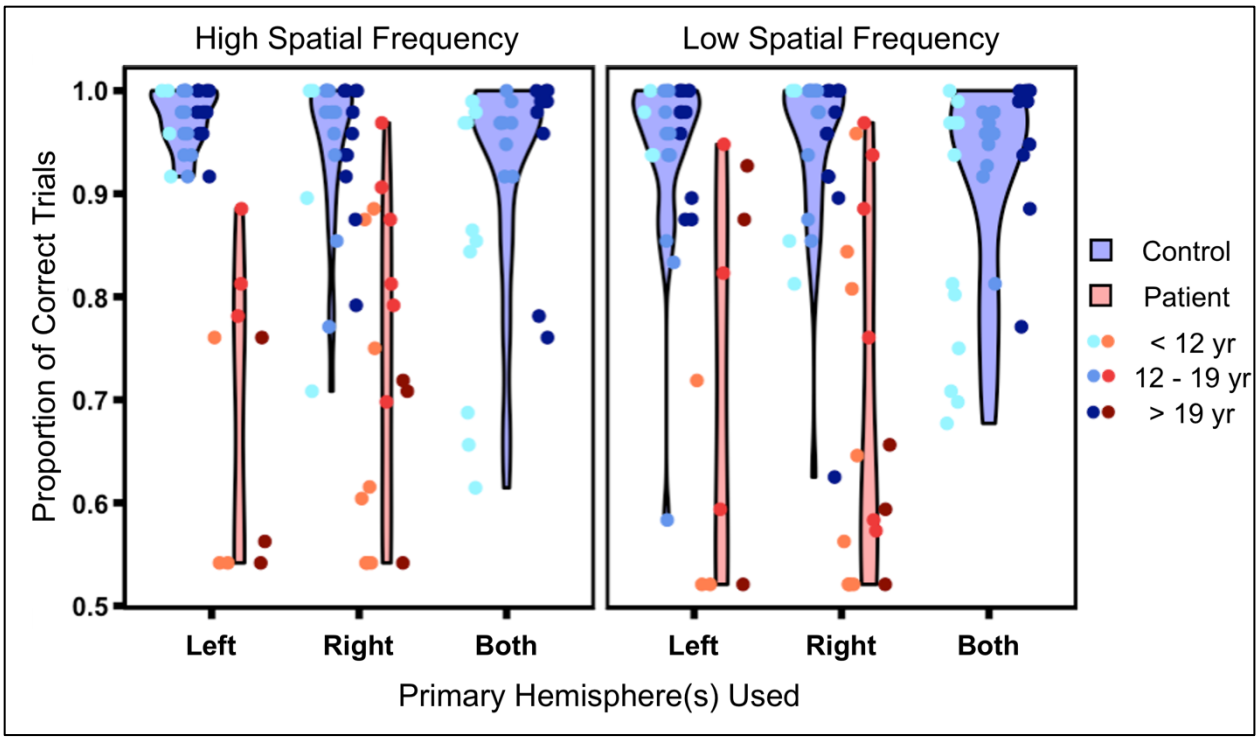

Figure 4. Violin plots show the distribution of accuracy values on the SF identification task for each group (patients and controls) by hemisphere used (left vs. right for patients and "one-hemisphere controls" viewing stimuli in the hemifields; both hemispheres for "central controls" viewing stimuli centrally) and stimulus category (HSF vs. LSF). Overlaid point plots show the individual values for each participant. To visualize any effect of age, points are separated by terciles of the age distribution, shown in different shades of blue (controls) and red (patients). Points are randomly jittered to minimize overlapping data. yr = years.

Patients vs. One-Hemisphere Controls

As above, the results from the three-way interaction are reported first. There was a significant three-way interaction effect of group x hemisphere used x stimulus category on accuracy ($t_{(103)} = 2.02$, $p = 0.05$, $d = 0.20$, BF = 1.70). To explore this interaction, separate linear mixed effects models were fit for each hemisphere, with group, stimulus category, and their interaction modeled as predictors of accuracy, and with age and participant again modeled as a covariate and random effect, respectively. Ultimately, there was no group x stimulus category interaction effect on accuracy for either the LH ($t_{(36)} = 1.55$, $p = 0.13$, $d = 0.26$, BF = 2.67) or RH ($t_{(44)} = 1.17$, $p = 0.25$, $d = 0.18$, BF = 4.81). However, importantly, patients had lower accuracy than controls: there was a significant main effect of group when using either the LH ($t_{(61)} = 6.12$, $p < 0.01$, $d = 0.79$, BF = $1.35*10^{-7}$) or RH ($t_{(61)} = 6.91$, $p < 0.01$, $d = 0.89$, BF = $2.88*10^{-6}$; see

Fig. 4) that was not qualified by stimulus category. In fact, there was no significant main effect of stimulus category on accuracy when using either the LH ($t_{(36)}$ = 1.59, p = 0.12, d = 0.27, BF = $1.49*10^1$) or RH ($t_{(44)}$ = 0.17, p = 0.86, d = 0.03, BF = $3.55*10^1$). Last, there was no significant main effect of age on accuracy when using either the LH ($t_{(36)}$ = 0.57, p = 0.58, d = 0.09, BF = 7.24) or RH ($t_{(44)}$ = 0.06, p = 0.96, d = 0.01, BF = 9.37). Altogether, the main takeaway is that patients showed lower accuracy on the task compared to controls, independent of both hemisphere used and stimulus category.

To elucidate the atypical performance profile per individual patient, each patient's accuracy per condition was compared to the respective distribution of accuracy of controls (while adjusting for age as a covariate). The proportions of each patient group (LH and RH) showing deficits compared to each the LH and RH of controls (ranging from 22 to 53%) are reported in the first two rows of Table 2 and are largely consistent with the inferential analyses showing general deficits in SF identification across patients.

Table 2. Individual patient accuracy on the SF task compared to distributions of controls using primarily the LH, RH, or both hemispheres. Each cell shows the percentage of patients in each group who showed an accuracy deficit compared to a given control distribution. Rows indicate the control distribution of comparison, and columns indicate the patient group and stimulus category.

	Patients with LH		**Patients with RH**	
	HSF	**LSF**	**HSF**	**LSF**
Controls Using Primarily LH	22.22%	44.44%	35.29%	52.94%
Controls Using Primarily RH	22.22%	44.44%	41.18%	52.94%
Controls Using Both Hemispheres	22.22%	44.44%	17.65%	52.94%

While accuracy reflects an individual's ability to recognize a stimulus of a given SF, it does not directly measure relative sensitivity to detecting different SFs. Sensitivity may be a better proxy for inferring whether a hemisphere is "tuned" for distinguishing stimuli of varying SFs. Thus, a linear mixed effects model was fit with d' (sensitivity index to HSF vs. LSF; see Materials and Methods for details on calculation) as the dependent variable; group, hemisphere used, and their interaction as predictors; age as a covariate; and participant as a random effect.

As with accuracy, there was a significant main effect of group on d': patients showed a significantly lower sensitivity index to SFs compared to controls ($t_{(60)} = 6.52$, $p < 0.01$, $d = 0.84$, BF = $5.45*10^{-9}$; see Fig. S3) that was not qualified by hemisphere used. That is, there was no significant interaction effect of group x hemisphere used on d' ($t_{(69)} = 0.65$, $p = 0.52$, $d = 0.08$, BF = 7.25). Furthermore, as with accuracy, there was no significant main effect of hemisphere used ($t_{(27)} = 0.98$, $p = 0.34$, $d = 0.19$, BF = $4.67*10^{1}$) or age ($t_{(55)} = 0.03$, $p = 0.97$, $d < 0.01$, BF = 8.94) on d'.

Altogether, these results indicate that, independent of the resection side, patients were impaired on SF identification compared to controls using primarily one hemisphere, suggesting that a patient's single hemisphere is not obviously tuned for select SFs.

Patients vs. Central Controls Using Both Hemispheres

Patients had lower accuracy on the task not only compared to one-hemisphere controls (as described above), but also to central controls: there was a significant main effect of group on accuracy ($t_{(78)} = 6.12$, $p < 0.01$, $d = 0.69$, BF = $8.76*10^{-6}$; see Fig. 4 for the central control data under "both hemispheres") that was not qualified by stimulus category. That is, there was no significant group x stimulus category interaction effect on accuracy ($t_{(57)} = 0.08$, $p = 0.94$, $d = 0.01$, BF = 10.6). Less importantly, there also was no significant main effect of stimulus category ($t_{(57)} = 0.42$, $p = 0.68$, $d = 0.06$, BF = $9.27*10^{1}$) or age ($t_{(57)} = 1.48$, $p = 0.15$, $d = 0.20$, BF = 3.65) on accuracy.

To test whether patients' accuracies differed from controls' as a function of the side of resection, separate linear mixed effects models were fit for patients with only a LH and those with only a RH. Group, stimulus category, and their interaction were modeled as predictors of accuracy, with age and participant modeled, once again, as a covariate and random effect, respectively. Independent of the resection side, patients had lower accuracy compared to controls: there was a significant main effect of group on accuracy for each the LH ($t_{(60)} = 4.64$, p

358 < 0.01, d = 0.60, BF = $3.33*10^{-4}$) and RH ($t_{(63)}$ = 5.79, p < 0.01, d = 0.73, BF = $1.34*10^{-4}$) that
359 was not qualified by stimulus category. That is, there was no significant group x stimulus
360 category interaction effect on accuracy for either the LH ($t_{(40)}$ = 0.96, p = 0.34, d = 0.15, BF =
361 5.69) or RH ($t_{(48)}$ = 0.82, p = 0.42, d = 0.12, BF = 7.00). As before, there also was no significant
362 main effect of stimulus category on accuracy for either the LH ($t_{(40)}$ = 0.43, p = 0.67, d = 0.07, BF
363 = $5.09*10^{1}$) or RH ($t_{(48)}$ = 0.47, p = 0.64, d = 0.07, BF = $3.42*10^{1}$). Last, while there was a
364 significantly positive main effect of age on accuracy for the LH ($t_{(40)}$ = 2.31, p = 0.03, d = 0.37,
365 BF = $7.26*10^{-1}$), there was no such main effect for the RH ($t_{(48)}$ = 1.33, p = 0.19, d = 0.19, BF =
366 4.10). These results were further validated by comparing each patient's accuracy per condition
367 to the respective distribution of accuracy of controls (proportion of patients with deficits ranging
368 from 22 to 53%), as reported in the last row of Table 2.
369 Last, a general linear model of group and age predicting d' revealed that patients
370 showed lower sensitivity to SFs compared to central controls. There was a significant main
371 effect of group on d' ($t_{(54)}$ = 6.76, p < 0.01, d = 0.92, BF = $1.99*10^{-7}$; see Fig. S3), as well as a
372 significantly positive main effect of age ($t_{(54)}$ = 2.14, p = 0.04, d = 0.29, BF = $7.50*10^{-1}$). Thus,
373 altogether, patients overall showed atypical SF identification/tuning compared not only to the
374 controls using primarily one hemisphere, but also to the central controls using both.
375
376 Relationship Between Word and Face Recognition and Spatial Frequency Identification
377 While there were largely no differences in word and face recognition between patients
378 and one-hemisphere controls, patients were impaired on both stimulus categories compared to
379 central controls using both hemispheres. Patients also showed deficits in SF processing,
380 suggesting that their single hemisphere was not tuned for this low-level visual information that
381 contributes to word and face recognition (Brederoo et al., 2020; Hsiao and Lam, 2013;
382 Woodhead et al., 2011). To explore the direct relationship between patients' word/face
383 recognition and SF processing, correlations between patients' accuracies across the word/face

and SF tasks were computed (see Fig. 5). The correlation analysis could not be reliably performed with the data from controls, as their accuracy was approaching ceiling (the likely explanation for why there was no hemisphere used x stimulus category interaction above; see Fig. 4 for data distribution).

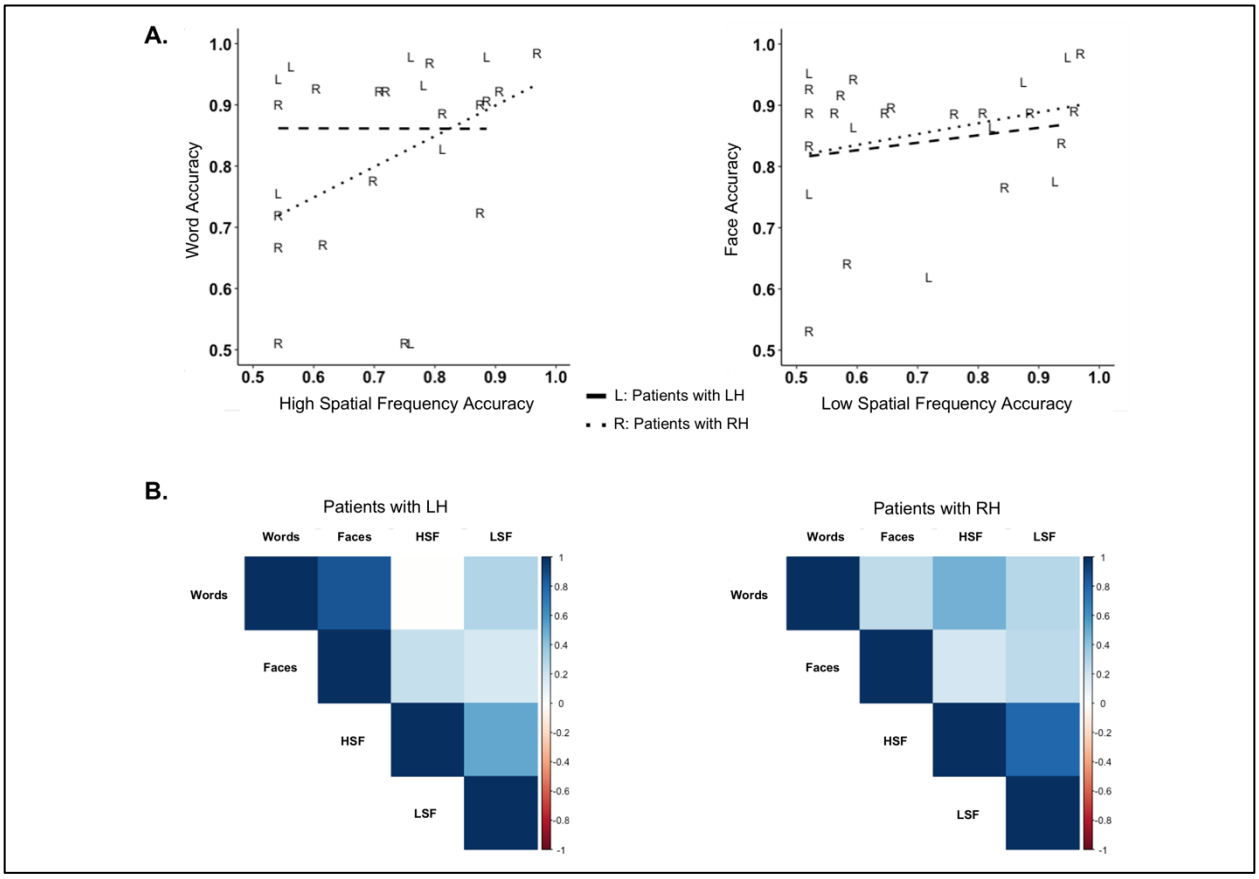

Figure 5. A: Plots of the correlation of accuracy (proportion of correct trials) on word and high spatial frequency trials (left panel) and face and low spatial frequency trials (right panel). Each point represents an individual patient. **B**: Correlation matrices for patients with a left (left panel) or right (right panel) hemisphere, with color indicating the magnitude of the correlation. LH = left hemisphere; RH = right hemisphere; HSF = high spatial frequency; LSF = low spatial frequency.

There was no significant correlation between accuracy on word and HSF trials among patients with only a LH ($r < 0.01$, $t_{(6)} = 0.01$, $p = 1.00$, $d < 0.01$) or RH ($r = 0.48$, $t_{(15)} = 2.09$, $p = 0.05$, $d = 0.54$). There also was no significant correlation between accuracy on face and LSF trials among patients with only a LH ($r = 0.18$, $t_{(6)} = 0.45$, $p = 0.67$, $d = 0.18$) or RH ($r = 0.27$, $t_{(15)} = 1.07$, $p = 0.30$, $d = 0.28$). Less relevant are the remaining correlations, as a correlation would not be predicted between either word and LSF trials or face and HSF trials (Ossowski and

Behrmann, 2015). There was no significant correlation between accuracy on word and LSF trials among patients with only a LH (r = 0.29, $t_{(6)}$ = 0.75, p = 0.48, d = 0.31) or RH (r = 0.29, $t_{(15)}$ = 1.16, p = 0.27, d = 0.30). Additionally, there was no significant correlation between accuracy on face and HSF trials among patients with only a LH (r = 0.24, $t_{(6)}$ = 0.60, p = 0.57, d = 0.24) or RH (r = 0.18, $t_{(15)}$ = 0.72, p = 0.48, d = 0.19). Thus, overall there was little association between performance on the word/face and SF tasks, suggesting no obvious association between the SF tuning of a patient's single hemisphere and that patient's word and face recognition abilities.

Discussion

Canonically, the LH and RH are considered to play important (albeit not exclusive) roles in word and face recognition, respectively (Behrmann and Plaut, 2020, 2015). The LH and RH are also tuned for identifying HSF and LSF stimuli, respectively (Hellige et al., 2010; Kauffmann et al., 2014; Sergent and Hellige, 1986), which is thought to contribute to or perhaps even underlie hemispheric superiorities for word and face perception (Brederoo et al., 2020; Hsiao and Lam, 2013; Woodhead et al., 2011). However, these hemispheric profiles emerge over development (Dehaene et al., 2010; Ossowski and Behrmann, 2015; Scherf et al., 2007), begetting the question of whether development with only a single hemisphere affects the ability to recognize words and faces. Moreover, is this developmental process equivalent if the single hemisphere is the left or the right?

In this study, a large group of hemispherectomy patients who had previously undergone surgery during childhood for pharmacoresistant epilepsy treatment were tested on tasks of word/face recognition and SF identification. To these authors' knowledge, there has not been a detailed investigation of the visual behaviors of such a large group of patients to date. Here, patients were compared to controls viewing stimuli presented either in a single hemifield (thereby engaging primarily a single hemisphere) or at central fixation (thereby allowing deployment of both hemispheres). Three principal findings were revealed across group and

individual case analyses. First, patients exhibited comparable word and face recognition abilities to those of controls using primarily one hemisphere, independent of the side of resection. Second, patients had lower accuracy on word and face recognition compared to central controls viewing stimuli foveally and using both hemispheres. Finally, patients exhibited lower accuracy and sensitivity on SF identification compared to both one-hemisphere and central controls, and patients' SF accuracy did not correlate with word or face recognition accuracy. Altogether, the findings suggest that the single preserved hemisphere in these childhood resection patients can support both word and face recognition. However, the patients show diminished performance relative to two intact hemispheres in matched controls. This diminution might partly be attributed to atypical hemispheric tuning for select SFs.

Development with a single hemisphere can support both word and face recognition

In the current study, patients with only a single hemisphere performed as well as controls primarily using one hemisphere. This is consistent with prior work showing not only intact general cognitive functioning in hemispherectomy patients (Moletto et al., 2018; Pulsifer et al., 2004; van Empelen et al., 2004), but also intact literacy following left hemispherectomy (de Bode et al., 2015). And notably, for both word and face recognition, participants showed the expected LH and RH superiorities for words and faces (Behrmann and Plaut, 2020, 2015), independent of group. Thus, patients with only a LH conceivably have better word recognition than patients with only a RH. Similarly, patients with only a RH would appear to have better face recognition than those with only a LH. However, development with a single hemisphere appears to support the recognition of *both* stimulus categories: patients with only a LH or RH showed no significant deficits on either task compared to one-hemisphere controls using primarily either their LH or RH.

The current results are consistent with findings from children with more circumscribed resections: children with VOTC resections not only evince co-existent neural representations for

words and faces in the unresected hemisphere, but also demonstrate typical visuoperceptual profiles (Liu et al., 2019, 2018). Furthermore, post-operative changes in functional connectivity in the intact hemisphere of pediatric VOTC resection patients may reflect both plasticity and competition for representation of multiple visual categories (Maallo et al., 2020). But in these relatively focal resection cases, residual ipsilesional tissue also shows some neural responsivity indicating that post-surgical performance may be a result of changes within the resected hemisphere (Liu et al., 2019, 2018). The current study of hemispherectomy patients, in contrast, offers a more explicit and dramatic demonstration of plasticity in the contralesional hemisphere, given the near to complete absence of ipsilesional cortex. Additionally, although patients here underwent surgery at various ages (see Materials and Methods), the resected hemisphere may well have been non-functional pre-surgically due to the nontrivial underlying pathology that necessitates a hemispherectomy (Kim et al., 2018). Future work should employ neuroimaging in this patient population to confirm these plastic changes for word and face representation in the contralesional hemisphere.

The intact word and face recognition in pediatric hemispherectomy patients is most remarkable considering the notable deficits that *adult* neuropsychology patients experience after more focal and circumscribed lesions in VOTC. Numerous case reports and studies have made clear that adults with a left focal (and even, small) lesion are dramatically impaired at word-reading (Behrmann et al., 1990; Cohen et al., 2003; Damasio and Damasio, 1983). Additionally, those with a right focal lesion (even as small as 990 mm^3; Konen et al., 2011) are, sometimes even profoundly, impaired at face recognition (Albonico and Barton, 2019; Gauthier et al., 1999). Quantifying these acquired impairments, Behrmann and Plaut (2014) reported that adults with a focal LH lesion took roughly 100 times longer (on two separate experiments) to read words of increasing lengths than matched non-neurological controls. Consistently, prosopagnosic adults after a focal RH lesion made roughly ten times more errors than matched controls on two different experiments of face recognition. These neuropsychological findings are

compatible with experiments in typical individuals who demonstrate LH and RH superiorities for word and face recognition, respectively (Hasson et al., 2002; Maurer et al., 2008; Rossion et al., 2003). On the other hand, these hemispheric superiorities appear to emerge over development and are not fully mature in children (Dehaene et al., 2010; Scherf et al., 2007). In childhood, it is conjectured that faces are initially represented bilaterally (Hildesheim et al., 2020). Only over time, as a result of the pressure associated with literacy acquisition, does word representation come to compete for representation in the LH (Dehaene-Lambertz et al., 2018; Dundas et al., 2014; Nordt et al., 2020). The current study suggests that, with plasticity in childhood, the potential for representing words and faces may be sufficiently malleable such that one hemisphere can, in fact, do double duty.

The question to be answered then is, what is the nature of the plasticity that gives rise to the relative competence of the single hemisphere? One possible answer is that the function typically subserved by the resected hemisphere arises de novo in the preserved hemisphere. An alternative, more parsimonious and more tractable explanation is that the bilateral representation for words and faces plays the critical role: as argued previously, although there are hemispheric superiorities for word and face representations in the LH and RH, respectively, the LH and RH have some competence in word and face processing too, albeit to a lesser degree (Behrmann and Plaut, 2020, 2015, 2013). For example, despite the stronger respective neural responsivity to words and faces in the LH and RH, there is nonetheless some appreciable bilateral activity for both stimulus categories (Appelbaum et al., 2009; Hasson et al., 2002; Matsuo et al., 2015). Furthermore, while patients with focal left and right lesions largely show respective impairments in word and face recognition, they can show deficits in both, often in relation to task difficulty (Asperud et al., 2019; Behrmann and Plaut, 2014; Gerlach et al., 2014). This weighted asymmetry of the hemispheres for word and face processing lends itself to the recruitment and optimization of the less robust representations in the preserved hemisphere once the “preferred” hemisphere (LH for words and RH for faces) is no longer functional.

Development with a single hemisphere then, may capitalize on the dual (weighted) LH and RH capabilities, with both word and face representations emerging with experience in the evolving, plastic preserved hemisphere. The remaining question then is what underlying processes necessitate the contribution of *both* hemispheres to enhance word and face recognition?

Spatial frequency tuning may underlie the two-hemisphere advantage for word and face recognition

The hemispheric superiorities for words and faces are thought to be related to, and perhaps benefit from, hemispheric tuning for HSF and LSF visual input, respectively (Brederoo et al., 2020; Hsiao and Lam, 2013; Woodhead et al., 2011). Despite their relatively intact word and face recognition capacity, hemispherectomy patients' classification of HSF vs. LSF stimuli is atypical compared to both control groups. Furthermore, patients' performance on word and face recognition is not correlated with their ability to identify SFs (although this must be qualified by the fact that the same analysis could not be justifiably run in the controls who performed largely at ceiling). Why might patients show intact word and face recognition, but atypical SF tuning? The answer to this may be related to resection of primary and secondary visual cortex, which are not chiefly implicated in word and face recognition but do encode SF information (Musel et al., 2013). Occipital resection almost always results in a permanent post-operative hemianopia (Kim et al., 2018; Liu and Behrmann, 2017). This suggests that the contralesional occipital lobe, which is sensitive to SF information (Musel et al., 2013; Peyrin et al., 2004), is not reorganized in such a way as to compensate for its resected homologue. Thus, perhaps posterior visual areas do not reorganize to the extent that more anterior visual areas do: this may explain why patients' word and face recognition is preserved while SF identification is impaired. Future work could examine SF sensitivity in each focal temporal and focal occipital resection cases to determine if preservation of occipital cortex is in fact critical for typical SF tuning.

At the same time, while intact hemispheric tuning for specific SF ranges may not be strictly necessary for word and face recognition, it may confer an advantage. Word and face recognition rely more on HSF and LSF information, respectively, but both perceptual encoding schemes are arguably beneficial for recognition of each words and faces (Brederoo et al., 2020; Hsiao and Lam, 2013). In fact, the extent to which the two hemispheres are lateralized for word and face recognition is correlated with the extent of differential SF tuning across the two hemispheres (Brederoo et al., 2020). Moreover, adult patients with LH damage show deficits in HSF processing that co-exist with deficiencies in recognizing both orthographic and non-orthographic complex stimuli (Roberts et al., 2013). Meanwhile, adult left-lesion alexia patients exhibit pronounced deficits even in recognizing line-drawn faces, suggesting that HSF information is advantageous for face processing (Albonico and Barton, 2017). Thus, utilization of both HSF and LSF information from the two hemispheres likely synergistically contributes to word and face recognition.

Conceivably, one might imagine that patients who develop with only a single hemisphere have a SF tuning function that is either atypically broad (with sensitivity across a large range of frequencies) or atypically narrow (with inferior sensitivity resulting from a smaller range of frequencies). Here, patients showed inferior SF sensitivity (measured as d') relative to controls, suggesting that the tuning function is narrow. This is consistent with the findings on the word and face recognition tasks: if the tuning function were broad, patients' performance would have been comparable to central controls using both hemispheres (and differential SF tuning). But patients only showed comparable word/face recognition accuracy to one-hemisphere controls. Thus, patients' SF sensitivity may be broad enough to sufficiently *support* word/face recognition, but the absence of broad SF tuning that two hemispheres typically confer may place limitations on category recognition.

Conclusion

555 Childhood hemispherectomy patients showed comparable word and face recognition to
556 controls using primarily one hemisphere but were impaired relative to controls using both
557 hemispheres on both word and face recognition. This outcome leads to the conclusion that,
558 perhaps via mechanisms of plasticity, one hemisphere appears to support, but is suboptimal for,
559 word and face recognition. The SF tuning of the two hemispheres may explain the advantage of
560 controls utilizing both hemispheres. Hemispherectomy patients appear to not develop typical or
561 compensatory SF tuning of the preserved single hemisphere based on deficient SF
562 identification/sensitivity of HSF and LSF visual input. So, while hemispherectomy patients can
563 perform word and face recognition sufficiently, their performance compared to controls with two
564 intact hemispheres may be limited due to atypically narrow SF tuning. This is one of the first
565 investigations to examine word/face and SF lateralization in pediatric patients with a single
566 hemisphere. Future work might examine more focal pediatric resection cases to explore what
567 specific lobes or anatomical regions support word and face recognition and confer two-
568 hemisphere controls' advantages on these processes. This investigation thus lays the
569 foundation for neuroimaging and/or electrophysiological studies exploring deployment of one vs.
570 two hemispheres for visual category recognition.
571
572 **Materials and Methods**
573 Participants
574 Twenty-six English-speaking patients with childhood hemispherectomy or
575 hemispherotomy (see Kim et al., 2018 for distinction; 17 with left resections and 9 with right
576 resections; median age = 15.0 years; median absolute deviation (MAD) of age = 8.9 years; 12
577 females, 14 males) were recruited for this study. Handedness could not be established in this
578 sample given that the hemiparesis (Kim et al., 2018; van Empelen et al., 2004) may have
579 resulted in a switch away from native handedness. In addition, 127 right-handed and native-
580 English-speaking controls (median age = 14.0 years; MAD of age = 8.9 years; 67 females, 60

581 males) participated. Not every participant completed all experimental tasks, and sample sizes
582 for each task and task condition are denoted below. Patients were recruited with the assistance
583 of the Brain Recovery Project: Childhood Epilepsy Surgery Foundation
584 (https://www.brainrecoveryproject.org/). Data assessing word/face processing from 66 typically
585 developing children and adult controls were previously collected by Dundas et al. (2013), and
586 data assessing SF processing from 15 adult controls were previously collected by Ossowski and
587 Behrmann (2015); data from an additional 46 controls (assessing word, face, and/or SF
588 processing) were collected from the local community and the Carnegie Mellon University (CMU)
589 participant pool, for the purpose of the current investigation.
590 There were two control groups: "*one-hemisphere controls*" who viewed stimuli in the
591 hemifields (thereby restricting initial processing to one hemisphere), and "*central controls*" who
592 viewed stimuli at central fixation as did the patients (thereby equating viewing conditions). To
593 confirm that groups were age-matched, for each task (word/face recognition and SF
594 identification), a logistic regression was fit with group (all patients vs. each control group—one-
595 hemisphere and central controls—in separate regressions) as the dependent variable and age
596 as the predictor. For the word and face recognition tasks, age was not predictive of group for
597 either the patient vs. one-hemisphere control ($z_{(89)} = 0.96$, $p = 0.34$, $d = 0.10$, BF = 6.07) or
598 patient vs. central control ($z_{(54)} = 0.30$, $p = 0.76$, $d = 0.04$, BF = 7.15) group comparisons. For
599 the SF task, age was also not predictive of group for either the patient vs. one-hemisphere ($z_{(51)}$
600 $= 1.35$, $p = 0.18$, $d = 0.19$, BF = 2.78) or patient vs. central control ($z_{(55)} = 0.15$, $p = 0.88$, $d =$
601 0.02, BF = 7.46) group comparisons. Details regarding the nature of patients' surgeries and
602 demographic/clinical information were reported by participants or participants' guardians.
603 Patient profiles are described in Table 3. The sample size was not sufficiently large to test
604 appropriately for the effects of clinical variables (such as age at surgery or efficacy of seizure
605 treatment) on the primary dependent measures in this investigation, but it would be informative
606 to conduct these analyses in future studies with larger sample sizes.

Table 3. Patient information. Some patients had multiple surgeries to complete the hemispherectomy: the approximate ages at the first and last surgery are reported. W = word, F = face, and SF = spatial frequency tasks.

Age	Gender	Surgery Side	~Age at First Surgery (years)	~Age at Last Surgery (years)*	Post-Surgical Seizures	Tasks Performed
6	Female	Right	3	-	No	W, F, SF
8	Male	Left	1	-	No	W, F, SF
8	Female	Right	0	-	Yes	SF
8	Female	Left	0	5	Yes	W, SF
8	Female	Left	0	1	No	W, F, SF
8	Female	Left	0	1	No	W, F, SF
9	Female	Right	0	2	No	W, F, SF
9	Female	Left	7	-	No	W, SF
9	Male	Left	4	-	No	W, SF
10	Male	Left	4	-	No	W, SF
11	Female	Left	0	10	Yes	W, F, SF
13	Female	Right	1	-	No	W, F, SF
15	Male	Right	2	-	No	W, SF
15	Female	Right	9	-	No	W, F, SF
15	Male	Left	5	-	No	W, F, SF
16	Male	Left	4	-	Yes	W, F, SF
16	Male	Left	14	-	No	W, SF
17	Male	Left	4	7	No	W, F, SF
17	Female	Left	4	-	No	W, F, SF
18	Male	Left	6	-	No	W, F, SF
22	Female	Right	4	-	No	W, F, SF
23	Male	Right	0	-	No	W, F, SF
28	Male	Left	1	18-19	Yes	W, F, SF
31	Male	Left	4	16	No	W, F, SF
34	Male	Right	11	27-28	No	W, F, SF
38	Male	Left	1	-	Yes	W, F, SF

*While two participants underwent initial surgery during childhood, the full hemispherectomy/hemispherotomy was not completed until adulthood (at 18-19 and 27-28 years). Excluding these participants in the analyses did not affect the primary interpretation of the results.

The experimental procedures were reviewed and approved by the CMU Institutional Review Board. Informed consent was acquired from all adult participants. Child participants gave informed assent, where possible, and their guardians provided informed consent.

Stimuli

Words

Pairs of four-letter gray words were presented in Arial font against a black background. The words in each pair differed by a single letter (for example, “tack” vs. “tank”). The second letter differed in approximately half of word pairs, and the third letter differed in the approximate remaining half, and words were chosen to be age-appropriate for young readers. For hemifield

presentations (from Dundas et al. (2013)), stimuli were shown at an estimated distance of 50 cm from the observer. These stimuli were approximately 1 cm tall by 3 cm wide, and thus the estimated respective subtended visual angles were 2 x 3°, respectively. For central presentations, stimuli were shown at an estimated distance of 60 cm. These stimuli were approximately 2 cm tall by 4 cm wide, with estimated respective subtended visual angles of 2 x 4°.

Faces

Grayscale neutral-expressive, forward-facing face stimuli from the Face Place Database (Righi et al., 2012) were also presented against a black background. Stimuli were edited to remove hair. For sessions with hemifield presentations (from Dundas et al. (2013)), stimuli were shown at an estimated distance of 50 cm from the observer. These stimuli were approximately 4 cm tall by 3 cm wide, with estimated respective subtended visual angles of 5 x 3°. For central presentations, stimuli were shown at an estimated distance of 60 cm. These stimuli were approximately 3 cm tall by 4 cm wide, with estimated respective subtended visual angles of 3 x 4°.

Gabor Patches

Two Gabor patches (that is, sinusoidal gratings with a Gaussian envelope) were generated with MATLAB (MathWorks), one with a (high) SF of 6 cpd and another with a (low) SF of 1.5 cpd. Each patch's contrast level was 0.3. Patches were presented against a black background in either the vertical or horizontal orientation per trial (randomly, approximately half of trials for each orientation). In sessions from Ossowski and Behrmann (2015), stimuli were shown at an estimated distance of 40 cm from the observer. Stimuli were approximately 4 cm tall by 3 cm wide, with estimated respective subtended visual angles of 6 x 4°. For all remaining

data collected for the sole purpose of the current investigation, stimuli were shown at an estimated distance of 60 cm. These stimuli were approximately 6 cm tall by 4 cm wide, with estimated respective subtended visual angles of 6 x 4°.

Procedures

Word and Face Recognition Tasks

Participants viewed stimuli presented on a laptop with either E-Prime (Psychology Software Tools; as in Dundas et al. (2013) and Ossowski and Behrmann (2015)) or the Psychophysics Toolbox (Brainard, 1997) in MATLAB (MathWorks; participants from the current investigation; see Fig. 1). A randomly jittered 1500 to 2500 ms interval separated trials, during which a fixation cross was displayed. Per trial, participants viewed one stimulus (either a word or a face) for 750 ms at central fixation (long enough for younger children to encode it). After a 150 ms interval during which a fixation cross was displayed, they then saw a second stimulus (of the same stimulus category: words or faces) for 150 ms (an interval too brief to reasonably saccade, thus ensuring stimulus presentation to one hemifield for one-hemisphere controls). Participants were asked to report, with a key press, whether the two stimuli were the same or different. Pairings of keys with response types were approximately counterbalanced across participants. All participants were instructed to maintain fixation centrally at all times. Participants acclimated to the tasks by participating in a set of practice trials prior to the tasks. Feedback and encouragement were provided where appropriate.

Participants from Dundas et al. (2013; the one-hemisphere controls) completed six blocks of the task, with 32 trials per block. Half the blocks presented only word stimuli, while the remaining half presented only face stimuli (data from only the face blocks were available for one participant). The second stimulus in a matching pair was presented in participants' hemifields (at an eccentricity of approximately 5° from fixation). Additional participants (patients and central

controls) whose data were collected solely for the current investigation completed one to two blocks of the task, with 96 trials per block, with both stimuli presented centrally. In select cases where a participant did not complete a block (due to participant declining in the majority of such cases or technical failure), fewer than 96 trials were recorded. In total, 25 patients (17 with left resections and 8 with right resections) participated in the word recognition task, and 19 patients (12 with left resections and 7 with right resections) participated in the face recognition task. Moreover, a total of 94 controls participated in the word recognition task, 65 of whom viewed stimuli in the hemifields, and 29 of whom viewed stimuli at central fixation. A total of 92 controls participated in the face recognition task, 66 of whom viewed stimuli in the hemifields, and 26 of whom viewed stimuli at central fixation.

There was notably more one-hemisphere control data available than central control data. To verify that the conclusions were independent of sample size, a random sample from the one-hemisphere control data was selected that matched the sample size of the central control group. Performing the analyses with this reduced control sample along with the patient sample, there was still a significant hemisphere used x stimulus category interaction ($t_{(118)} = 2.31$, $p = 0.02$, $d = 0.21$, BF = 6.59) and no significant main effect of group ($t_{(119)} = 0.48$, $p = 0.63$, $d = 0.04$, BF = $1.70*10^4$). These results are consistent with those from the analyses on the full one-hemisphere control sample.

SF Identification Task

Using the same software described above, participants viewed Gabor patches one at a time for 20 ms each, with a randomly jittered 1500 to 2500 ms intertrial interval (see Fig. 3). Participants were asked to report, with a key press, whether the stripes/lines of a patch were narrow (that is, with HSF) or wide (with LSF), independent of orientation. Pairings of keys with response types were approximately counterbalanced across participants. As before, participants were instructed to maintain central fixation at all times, and exposure duration was sufficiently

699 brief that an eye movement was not possible. Participants acclimated to the tasks by
700 participating in several practice trials prior to the experimental trials. Feedback and
701 encouragement were provided where appropriate.

702 Participants from Ossowski and Behrmann (2015; all one-hemisphere controls)
703 completed two blocks of the task, with 96 trials per block. Stimuli were presented to the one-
704 hemisphere control group in participants' hemifields (at an eccentricity of approximately 5° from
705 fixation). The patients, one-hemisphere controls, and central controls whose data were collected
706 for the sole purpose of the current investigation completed one to two blocks of the task, with 96
707 trials per block. In select cases, fewer than 96 trials were recorded (due to participant declining
708 in the majority of such cases or technical failure). In total, 26 patients (17 with left resections and
709 9 with right resections) participated in this task. Moreover, a total of 58 controls participated in
710 this task, 27 of whom viewed stimuli in the hemifields, and 31 of whom viewed stimuli at central
711 fixation.

712

713 Data Analysis

714 Statistical analyses were conducted in R version 3.5.2 (R Core Team, 2018; using
715 default parameters unless otherwise specified) and MATLAB R2018b and R2019b
716 (MathWorks). Descriptive statistics for reporting of demographic data were computed with the R
717 package psych (Revelle, 2019). Linear mixed effects models were fit with the R packages lme4
718 (Bates et al., 2019, p. 4) and lmerTest (Kuznetsova et al., 2019), and *p*-values (rounded to two
719 decimal places, as were *t* statistics) were estimated using the Satterthwaite's degrees of
720 freedom (rounded to the nearest integer in the Results) method. Fixed effects were estimated
721 such as to optimize a log-likelihood function. All other models were fit using the glm function in
722 R (R Core Team, 2018). If an interaction effect was significant, the individual lower-order
723 interactions and/or main effects composing the interaction for that model were not
724 reported/interpreted. Cohen's *d* effect sizes for statistics were calculated with the R package

effectsize (Ben-Shachar et al., 2020), with the assumption that the statistic in question was derived from comparisons of dependent means. BFs were computed as *e* raised to half of the difference of the Bayesian information criterion (BIC) of the alternative model (including all effects of interest) and BIC of the null model (excluding the effect being tested), as described by Wagenmakers (2007). Pearson correlation coefficients and associated statistics were calculated using the cor.test function in R (R Core Team, 2018). For analysis of individual patients' deficits, *p*-values were computed using open-source statistical software provided by Crawford et al. (2011). Patients were classified as having a deficit if their *p*-value was below the Bonferroni corrected α criterion. d' was computed as the difference of the inverse of the standard normal cumulative distribution function of the hit rate and that of the false alarm rate. In instances where the hit rate was 100%, $(n-1)/n$ was substituted as the hit rate in the d' calculation, where n is the number of trials. Plots were generated in R with ggplot2 (Wickham et al., 2019), ggpubr (Kassambara, 2020), ggnewscale (Campitelli, 2020), and corrplot (Wei et al., 2017). Experiment and analysis code, as well as associated raw data, are available on KiltHub (CMU; digital object identifier: 10.1184/R1/12743276).

If a participant did not perform either the word or face task (see Table 3), their accuracy for the missing stimulus category was assigned to be the median of all accuracies for the given group, hemisphere used, and stimulus category. If a participant's accuracy was below 50%, that participant's accuracy was replaced with winsorization, such that the accuracy of that participant was computed as the minimum accuracy above 50% of all accuracies for the given group, hemisphere used, and stimulus category (low end of the distribution to avoid inflating the group result). Furthermore, on the SF task, if one accuracy value for a given SF was below 50% (averaged across hemifields for one-hemisphere controls), then the participant was presumed to have been primarily pressing one button: accuracy for both stimulus categories was winsorized to the minimum accuracy above 50% of all accuracies for the given group, hemisphere used,

750 and stimulus category. All inferential tests were performed on winsorized data; Crawford
751 statistics were calculated on the raw data.
752
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